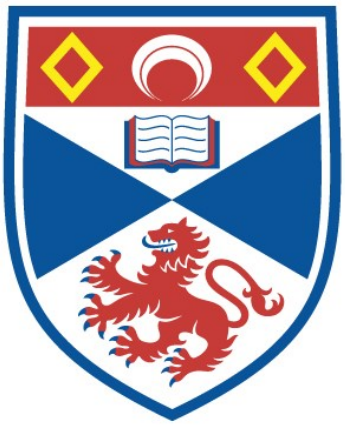
AN INVESTIGATION INTO THE PRIMARY PRODUCTIVITY OF THE ANTARCTIC MACRO-ALGA PHYLLOGIGAS GRANDIFOLIUS (A. & E.S. GEPP) SKOTTSB.

Robin M. Hastings

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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An Investigation into the Primary Productivity of the Antarctic macro-alga Phyllogigas grandifolius (A. & E.S. Gepp) Skottsb.

by

ROBIN M HASTINGS

Thesis presented for the degree of

Doctor of Philosophy

Gatty Marine Laboratory and
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ABSTRACT

The productivity of the large brown alga Phyllogigas grandifolius (A. & E.S. Gepp) Skottsb. has been studied over a period of $2\frac{1}{2}$ years. This alga is endemic to the Antarctic and circumpolar in distribution.

Photosynthesis was measured in situ using SCUBA. Uptake of ^{14}C-labelled sodium bicarbonate was used to obtain values for gross photosynthesis throughout the year, and by monitoring respiration at the same time using the Winkler technique a value for daily accretion could be found.

The curves for daily accretion showed only one mm maximum per season, that at the deeper of the two sites occurring later than at the shallow site, as the light levels reaching the deeper algae continued to increase.

Positive accretion expressed in $\mu gC.\ cm^{-2}.d^{-1}$ was observed only during the summer months. Maxima in 1974 were 70 $\mu gC.cm^{-2}.d^{-1}$ at the shallow site and 56 at the deep site.

Respiration was low throughout the year as a result of the small annual range of water temperature ($+1.5^{\circ}C$ to $-2^{\circ}C$). The mean respiratory rate was found to be 1.55 $\mu gC.cm^{-2}.h^{-1}$. Variation in the rate was observed along the length of the frond with the maximum occurring in the region of the meristem about 10cm. above the base of the frond.

In situ studies of frond growth showed a complete cessation of growth during the winter months but recommenced before the departure of the sea-ice. This and daylength appear to be the two main limiting factors of growth. Mean growth rate: 8.0mm. wk^{-1}.

With the growing season restricted to 6 months, the mean productivity for that season was found to be 2.4 g $C.m^{-2}.d^{-1}$, with a photosynthetic efficiency of 14%. In the winter this efficiency drops to 1%. These figures were obtained from bomb calorimetry studies.

Mannitol, the main storage product and primary respiratory substrate showed summer maxima of around 18% dry weight, falling to 2% during the winter.

Due to the irregular distribution of the alga, biomass estimates are rather subjective. One of the denser 'stands' of Phyllogigas gave a figure of 0.813 kg. m^{-2} and a Leaf Area Index of 4.5. Other LAI values were as low as 0.0028. The mean SLA was 0.075.

The net annual primary productivity was found to be 15.3 metric tons. $hectare^{-1}$ $year^{-1}$.

FRONTISPIECE

Phyllogigas Grandifolius at 6m. in Borge Bay, Signy Island

South Orkneys

DECLARATION

I hereby declare that the following thesis is based upon work carried out by me, that the thesis is my own composition and that it has not been previously presented for a higher degree.

The research was conducted at the British Antarctic Survey Base H, Signy Island, South Orkneys and at the Gatty Marine Laboratory, University of St. Andrews, and was supervised by Dr. E.A. Drew.

CERTIFICATE

I certify that ROBIN M. HASTINGS has spent twelve terms of research under my direction, that he has fulfilled the conditions of Ordinance General No. 12 and Resolution of the University Court 1967, No. 1., and that he is accordingly qualified to submit the accompanying thesis in application for the degree of Doctor of Philosophy.

CURRICULUM VITAE

I was educated at Bishop Vesey's Grammar School, Sutton Coldfield, West Midlands and Lancaster University. I graduated from there in 1972 with a B.A. (Hons.) in Biology of Organisms and immediately took up a post with the British Antarctic Survey as a Biologist. The field studies for this thesis were carried out during $2\frac{1}{2}$ years in the Antarctic (1972 to 1975) and the work was written up at the Gatty Marine Laboratory, St. Andrews (1975 to 1977).

ACKNOWLEDGEMENTS

I would like to thank the Director of the British Antarctic Survey, Dr. R.M. Laws, for allowing me to submit this work as a thesis for the Degree of Doctor of Philosophy.

My special thanks are due to Dr. E.A. Drew who supervised the work. His advice and instruction are gratefully appreciated.

Generous thanks are also due to my Section Head in B.A.S., Dr. R.B. Heywood for his continued interest in the work and much useful criticism.

To the many B.A.S. personnel at Signy Island, 1973 to 1975 I offer my grateful thanks, particularly Mr. Howard Bissell whose skill as a diver was a great asset to the work and to Peter Vane for many cold hours as boatman or linesman.

I would also like to thank my parents for their encouragement over the years and lastly my typist, Mrs. Christina Lamb, for producing a presentable thesis from my notes.

CONTENTS

CHAPTER 1

INTRODUCTION

I ALGOLOGY IN ANTARCTICA

With the exception of references to the giant kelp Macrocystis in the narratives of early explorers, nothing was known about the marine algae of the Antarctic and Subantarctic until the appearance in 1825 and 1826 of descriptions by Gaudichaud of the material collected during the 1817-1820 expedition by the French corvettes 'Uranie' and 'Physicienne'.

Another early effort to collect Antarctic algae was made in 1841 by J.D. Hooker, botanist-surgeon of the Erebus and Terror Expedition under Captain James Clark Ross. Hooker states in Flora Antarctica (vol. 9);

> "Two small islets were landed upon, one in lat. 71° 49'S, long. 170° 52'E, the other, Franklin Island in lat. 76°S, long. 168° 59'E, but neither of these spots presented the slightest trace of vegetation."

Hooker sent some of his plankton samples to the German diatomist Ehrenberg who published the first paper on Antarctic diatoms (1844). Since that date numerous phytoplankton investigations have been carried out, perpetuating the belief in the fertility of the Antarctic seas.

Montagne (1845), published an account of the flora observed by Dumont d'Urville's expedition to the Antarctic, during which he discovered Terre Adelie, correctly mapped the South Sandwich group and added more detail to Cook's chart of South Georgia, discovered in January 1775. While Cook was the first explorer sent with a specific task, namely to find the fabled 'Southern Continent', his voyage was primarily one of exploration and charting and no collecting was carried out.

In February 1900, sixty years after Ross, the first Ross Sea alga, Desmarestia willii Reinsch (reported as D. viridis Lam.) was collected from the same islands that Hooker landed on, by Borchgrevink's party. About this time, the 'Belgica' Expedition under de Gerlache was also collecting algal specimens. The collection was made by Racovitza but has never been worked up. (See de Wildeman, 1900, preliminary report). Other species, collected by the 'Southern Cross' British Antarctic Expedition near Cape Adare were:

Desmarestia aculeata (L) Lamour

D. rossii Hooker and Harvey

Ballia callitricha (C.Ag.) Kütz

Plocamium coccineum (Huds.) Lyngb.

In the list by Barton, no characteristics are given about these algae or their habitats.

The next collection of algae was again made in the Ross Sea sector, in Victoria Land by the British National Antarctic Expedition, under Captain R.F. Scott, with the 'Discovery', (1901-1904). Twelve species are reported; one of these, Iridaea micans Bory was collected on the ice of the bay between Black Island and White Island at the southern

end of McMurdo Sound on the 14th September 1902. A weathered, faded and fragmentary specimen, but fruiting. The other species were reported under the following names:

Off Cape Wadsworth, at Coulman Island:

Zonaria sp.

Lessonia grandifolia A.and E.S. Gepp

Desmarestia larveyana "

Gracilaria sp

G. simplex A. and E.S. Gepp

Plocamium coccineum (Huds.) Lyngb.

Delesseria quercifolia Bory

Phyllophora antarctica A. and E.S. Gepp

At Cape Adare:

Desmarestia larveyana A. and E.S. Gepp

Ectocarpus germinatus Hooker and Harvey

Gracilaria dumontioides A. and E.S. Gepp

Lessonia grandifolia "

Spongoclodium orthocladium "

Few ecological studies have been made on the coasts of Antarctica. Skottsberg (1906) made the first study during the Swedish National Antarctic Expedition, 1901-1903. His work was followed by that of Gain (1912) who distinguished:

"une région littorale comprise entre la plus haute

et la plus basse mer ..... à laquelle fait suite la région sub-littorale depuis le niveau des plus basses mers jusqu' à une quarantaine des metres limite extrême des Desmarestia ..... enfin la zone élittorale qui doit se terminer vers 150m correspondant à la limite extrême de la dispersion des algues."

In April, 1905 Anthony and Ethel S. Gepp published a list of Antarctic algae collected by R.N. Rudmose Brown in April 1904 at the South Orkney Islands during the Scottish National Antarctic Expedition under W.S. Bruce.

The most interesting specimen was a very large, unknown brown alga called Lessonia grandifolia n.sp. What seemed to be the same plant had also been collected on the coast of Victoria Land (above) in 1902 and as the South Orkney material was too fragmentary, the description was based on the former. Specimens were also collected by Skottsberg from South Georgia (April - June 1902) and from the west coast of the Antarctic peninsula (Graham Land then) in December 1902. Skottsberg's early work provided the first clear indication that there was, below the level of severe ice abrasion, a rich growth of large plants. Unfortunately the bulk of his collection was lost when the ship of the ill-fated Swedish Antarctic Expedition was sunk by pack-ice in 1903.

Skottsberg and Gepp worked on Lessonia grandifolia at the British Museum in 1906. The Gepps were of the opinion that there were two species, differing in lamina anatomy; one from Victoria Land - grandifolia and one from the South Orkneys - simulans. Continued study of the South Georgia material and additional specimens collected in 1909 convinced Skottsberg that it belonged to Gepp's Antarctic Lessoniae, but not to Lessonia, differing in external morphology and anatomical structure. Age differences,

he thought, had caused the anatomical variation, therefore he united the 'species' under a new genus, Phyllogigas and species, grandifolius.

Gain (1912) gives an account of the algae collected during Charcot's second expedition, 1908-1910.

The 'Terra Nova' Expedition (1910-1913) under Scott records Phyllogigas caught on the anchor in Robertson Bay off Cape Adare, 19th February 1911, and Leptosomia simplex (A. and E.S. Gepp, Kylin) brought up in an Agassiz trawl from a depth of 82-92m. Hylmo (1919) and Kylin and Skottsberg (1919) discuss further aspects of Antarctic algology of this period.

Since that date a large number of expeditions to the Antarctic have made collections of the marine flora providing much knowledge of the rich and varied communities to be found in these waters. About 500 species, representative of more than 190 genera have been reported from various localities in Antarctica. Samples taken in the Antarctic and Subantarctic have yielded more than 30 genera and 250 species of marine algae. Of the 30 genera, more than half are monotypic and appear endemic to the area. Also endemic to the region are many species belonging to genera represented in other parts of the world (Papenfuss, 1962).

The initiation of the 'Discovery' Investigations in 1925 heralded a new phase, stressing the dynamic aspects of Antarctic biology. Although these investigations were primarily concerned with whales and whaling, studies of the factors influencing their migration, food, feeding habits and breeding cycle, they in turn have led to an extensive programme of physical and biological oceangraphy resulting in the valuable 'Discovery Reports'. Although other expeditions have followed, credit goes to the 'Discovery' for initiating a continuous programme.

Since the International Geophysical Year (1957-1958) scientific investigation in Antarctic waters has expanded and is still gaining momentum. For a detailed chronological list of Antarctic expeditions see Roberts (1959).

The majority of primary productivity studies carried out in Antarctica have been on phytoplankton; these were by Hart (1934, 1942); Burkholder & Sieburth (1961); Klyashtorin (1961). Diatoms: Bunt (1963); Bunt (1964a,b); El Sayed et al (1964); Saijo & Kawashima (1964); Burkholder & Mandelli (1965); El Sayed & Mandelli (1965); Mandelli & Burkholder (1966); El Sayed (1967, 1968a); Dinoflagellates: Balech (1968); Diatoms: Hasle (1968).

Very little work has been done in this field on Antarctic macroalgae.

Productivity Studies in Algae

Plant growth results from the interaction of the metabolism of the plant with a number of complex environmental factors. This production by the plant may be measured in various ways. Westlake (1963) has given a comprehensive review of all aspects of plant productivity and the two main methods for determining annual productivity are critically assessed. These are the 'harvest' or increment cropping method (Penfound 1956; Odum 1973) and the measurement of the rate of photosynthesis. Biomass increment cropping is very useful in plant communities showing marked annual fluctuation of biomass and having few losses up to the seasonal maximum biomass. Short term photosynthetic rates have been measured in this work and these together with controlled laboratory studies give some indication of the ability of the plant to grow under varying environmental conditions.

The rate of photosynthesis gives an estimate of the performance of the plant and together with a knowledge of the rate of loss by respiration a figure for daily accretion and hence yearly production can be estimated. Autotrophic plants ultimately rely on the efficiency with which total solar energy is trapped and converted into organic materials. The net productivity achieved depends on the total solar energy available and those factors in the environment affecting the rate of photosynthesis. Rabinowitch (1956) outlines many of these factors and Thomas (1955) and Talling (1961) discuss photosynthesis under natural conditions.

The growth and productivity of littoral marine algae has been studied under field conditions by Gail (1922), Tschudy (1934), Printz (1939), Tikhovskaya (1940) and Levring (1947, 1966, 1967) using the Winkler oxygen technique developed by Gaarder and Gran (1927). Sargent and Lantrip (1952) measured the photosynthesis 'in situ' of various regions of Macrocystis pyrifera and from the data inferred that translocation of organic matter into the growing tips was necessary to support growth. Black (1950a,b) and Black and Dewar (1949) using pH and oxygen levels as a measure of photosynthesis attempted to correlate the seasonal growth of three Laminaria species with physical and chemical factors in the environment. Blinks (1955) and Kanwisher (1966) have also measured the photosynthesis of attached marine macrophytes under natural conditions. More recently, the C^{14} method for measuring photosynthesis 'in situ' introduced by Steemann-Nielsen (1952) has been used to study the rate of primary productivity in macrophytic algae.

Other parameters of growth such as stipe length, lamina length and expansion, biomass changes with depth and season and the growth of stages in the life cycle under natural conditions, have been correlated

with ecological factors by Parke (1948); Black (1950a,b); Conover (1958); Macfarland and Prescott (1959); Sundene (1962, 1964); Neushul and Haxo (1963a,b); Kain (1963-71); Bellamy and Whittick (1968); Norton and Burrows (1969a,b); Luning (1969a,b, 1970); Mann (1972a,b,); Kain (1976b).

Previous work has emphasised the importance of light intensity (Kain 1966; Levring 1966; John 1968; Whittick 1969; Drew et al 1972) and temperature (Kniep 1914; Harder 1915; Ehrke 1931; Sundene 1962, 1964; Tseng et al 1957, Kanwisher 1966; Newell and Pye 1968) whilst others have demonstrated the importance of interactions between the two factors and their combined effect on photosynthesis and respiration, (Tikhovskaya 1940; Levring 1966.

The studies in this thesis have centred upon measurements of photosynthesis over two seasons, using uptake of C^{14}-labelled sodium bicarbonate. These figures have been used to obtain an estimate of the annual productivity of Phyllogigas after allowing for respiratory losses. Seasonal variations in growth rate have been observed together with changes in dry weight and organic weight. The influence of environmental factors such as sea-ice, phytoplankton, light and temperature are discussed.

II THE ANTARCTIC ENVIRONMENT

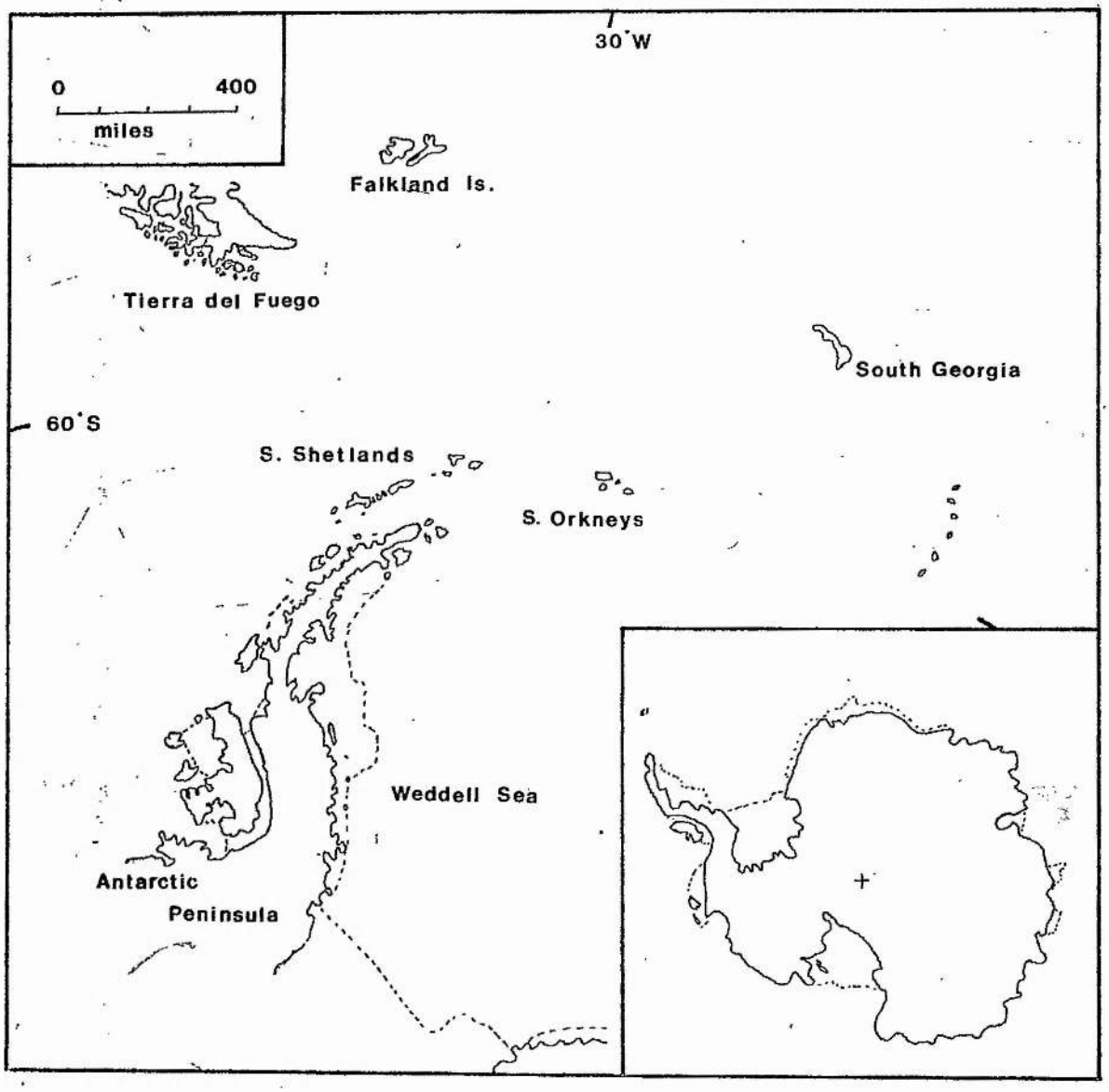
The Antarctic ice continent accounts for 5% of the total world coastline (Zaneveld, 1968). It is unique not only in being a large polar land mass, but also in being, perhaps, the most isolated of continents. This isolation from the continents of the Southern Hemisphere is enhanced by the Antarctic Convergence, formed when the north-moving Antarctic Surface Water sinks beneath the less dense south-flowing Subantarctic

Surface Water. It is a well-defined boundary between water masses of separate origins and as such is of great significance in the distribution of life in the sea. Although probably not an impassable barrier to marine organisms, it prevents the dispersal of species which are adapted to the conditions on one side but cannot maintain themselves permanently in the conditions on the other (Mackintosh 1946). More detailed accounts of the hydrology of the Southern Ocean are given by Deacon (1937, 1963) and Gordon (1967).

The isolation of the continent presents considerable logistic problems for any scientific programme and despite the upsurge of scientific investigation in Antarctic waters since 1957-58, information on predominantly sub-tidal marine flora remains very scattered and generally incomplete.

The most recent treatment of biogeography and ecology (Van Oye and van Mieghem, 1965) does not deal specifically with benthic marine algae, but a catalogue and bibliography of Antarctic and Sub-antarctic benthic marine algae, including distributional data, has been compiled by Papenfuss (1964). Exploratory ecological work recently carried out is beginning to change many older ideas about horizontal and vertical distributions of Antarctic marine plants (see Delepine 1966; Delepine, Lamb and Zimmermann 1966; Zaneveld, 1968). With the advent of SCUBA, the bulk of this new work, in common with sub-littoral studies elsewhere in the world, is being done by botanists using diving techniques to collect and observe the plants in situ.

Phytogeographically, it has been suggested that the Antarctic and Subantarctic can be regarded as a single province and Zinova (1958), Knox (1960) and others distinguish an Antarctic region bounded on the north by the Antarctic Convergence. Tabulation of the species of the Antarctic zone,



Map 1. The position of the South Orkney Islands in relation to the rest of Antarctica

based on type material listed in the catalogue by Papenfuss suggests an even higher degree of endemism, 35% (Zaneveld 1968) than that calculated by Zinova (1958) (25%).

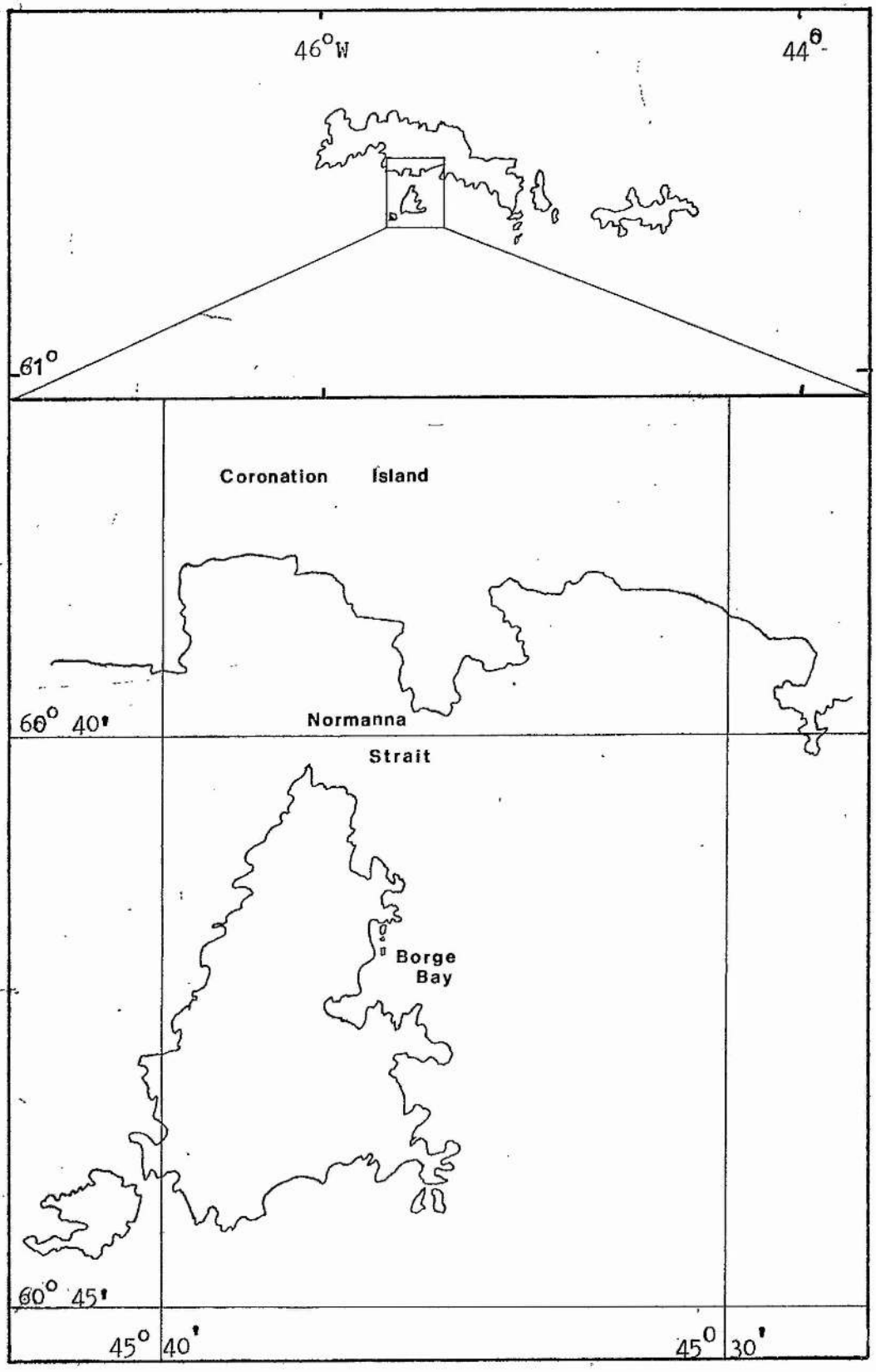
III THE SOUTH ORKNEY ISLANDS

Lying close to lat. 60°S and long. 45°W, the South Orkney Islands comprise two main and several small islands occupying a position on the Scotia Ridge about 1,440km (900 miles) south-east of Tierra del Fuego and 640km (400 miles) north east of the northern extremity of the Antarctic Peninsula. The largest island of the group, Coronation Island, is about 48km (30 miles) from east to west; to the south of its central part lies Signy Island (lat. 60° 43'S., long. 45°38'W.), where the British Antarctic Survey's station is situated. (See Map 2).

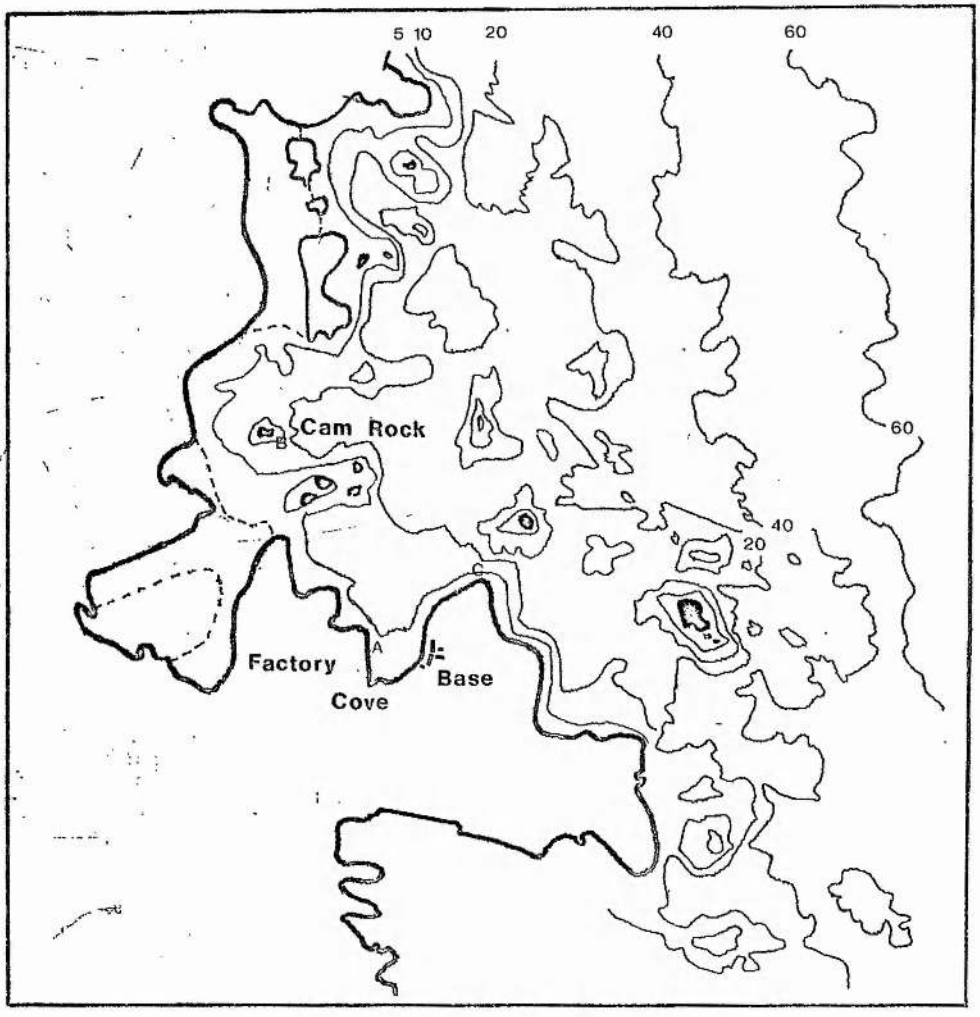
The South Orkneys thus lie in the maritime Antarctic zone of southern polar lands (Holdgate 1964, 1970), a zone confined mainly to the western coastal area of the Antarctic peninsula, but including offshore islands together with the island groups comprising the southern part of the Scotia Ridge, i.e. South Shetland, South Orkney and South Sandwich Islands, and also Bouvet Island and Peter I Island (See Map 1).

Signy Island - Physical

Signy Island, together with most of the islands of the Scotia Arc, is the remains of an early Mesozoic cordillera, breached during the late Cretaceous (Allen, 1966). The rocks of the island, quartz-mica-schists, amphibolites and marbles, are either Precambrian or early Cambrian in age (Adie, 1964; Matthews and Maling, 1967) and are sufficiently hard to provide a stable substrate for sessile organisms and to prevent colonisation by boring animals.



Map 2. Signy Island, South Orkneys



Map 3. Borge Bay, Signy Island, showing positions of the B.A.S. base and the 3 sampling sites:

A – Shallow site in Factory Cove
B – Deep site at Cam Rock
C – Site of winter lead (due N. of base) used in Respiration experiment.

Depth contours in metres

Signy Island lies immediately south of Coronation Island, the largest island in the group and is separated from it by the 1.6km wide Normanna Strait (Map 2). The island is triangular in shape, being 7km from north to south and 5km from east to west.

The central part of the island is formed by a plateau 213–244m (692–793 ft.) above sea level with several peaks rising to a maximum of 276m(897 ft.). The edge of the plateau is sharply defined and characterised by many small cirques, most of which terminate 30–61m (97–198 ft.) above sea level. Some of these cirques extend below sea level, for example Paal Harbour, a drowned cirque with depths exceeding 20m (65ft.) (See Appendix 'Diving Procedures'). Areas of lowland, occurring mainly on the east coast are covered with glacial drift. (Matthews and Maling, 1967) (See Map 2).

CHAPTER 2

THE PLANT AND ITS ENVIRONMENT

I PHYLLOGIGAS - THE SPECIES INVESTIGATED

Taxonomy, morphology and anatomy

The endemic Antarctic brown alga Phyllogigas grandifolius was first studied at the beginning of the century by A. and E.S. Gepp (1905), Skottsberg (1906, 1907) and Lucas (1919). Zinova (1959) advocated the establishment of a new order for Phyllogigas; Skottsberg and Neushul (1960) took a more cautious line in discussing its growth and development; on the basis of its gross morphology it was provisionally placed in the Laminariales since its reproductive structures were not then known.

Plates 1 to 4 show various aspects of the morphology of the alga. Plate 1 shows a young, pressed specimen of Phyllogigas, collected in February 1974 in 4.5m water at the shallow site (see Map, this chapter). The holdfast is flattened, lobed and branching (see plate 3) from which arise one or more flattened stipes, exhibiting dichotomous branching. The stipe merges indistinctly into a broad lamina, flattened in the same plane as the stipe. The laminae, as they mature, show signs of distal abrasion and generally lie flat over the sea-floor as no support is provided by the stipe. The drag of mature laminae frequently breaks the stipe, often leaving only one lamina per plant. (Plates 2 and 3).

THE PLATES

Plate 1. (Top left)

A young pressed specimen of Phyllogigas grandifolius, collected at the shallow site, Factory Cove in February 1974. To give an idea of scale, the lamina on the left has a maximum width of 7.7cm and length of 15.5cm. The flattened, dichotomously branching stipes can be clearly seen. Age: approximately 4 months.

Plate 2. (Bottom left)

Measurement of holes punched in the lamina of plant 5. Only the basal part of the lamina is shown. An impression of the size of the plant and its exposed situation is given. Photograph taken during winter.

Plate 3. (Top right)

First signs of new growth, late September 1974. New lobes of the holdfast are clearly seen, despite the continued presence of sea ice. The single, flattened stipe and lamina (cf. Plate 1) is the more usual case in mature plants. The elliptical nature of the holes punched in the lamina is well illustrated.

Plate 4 (Bottom right)

A mature plant (stipes and holdfast at bottom right) with several laminae lying coiled across the sea floor. The massive nature of the laminae is clearly seen.

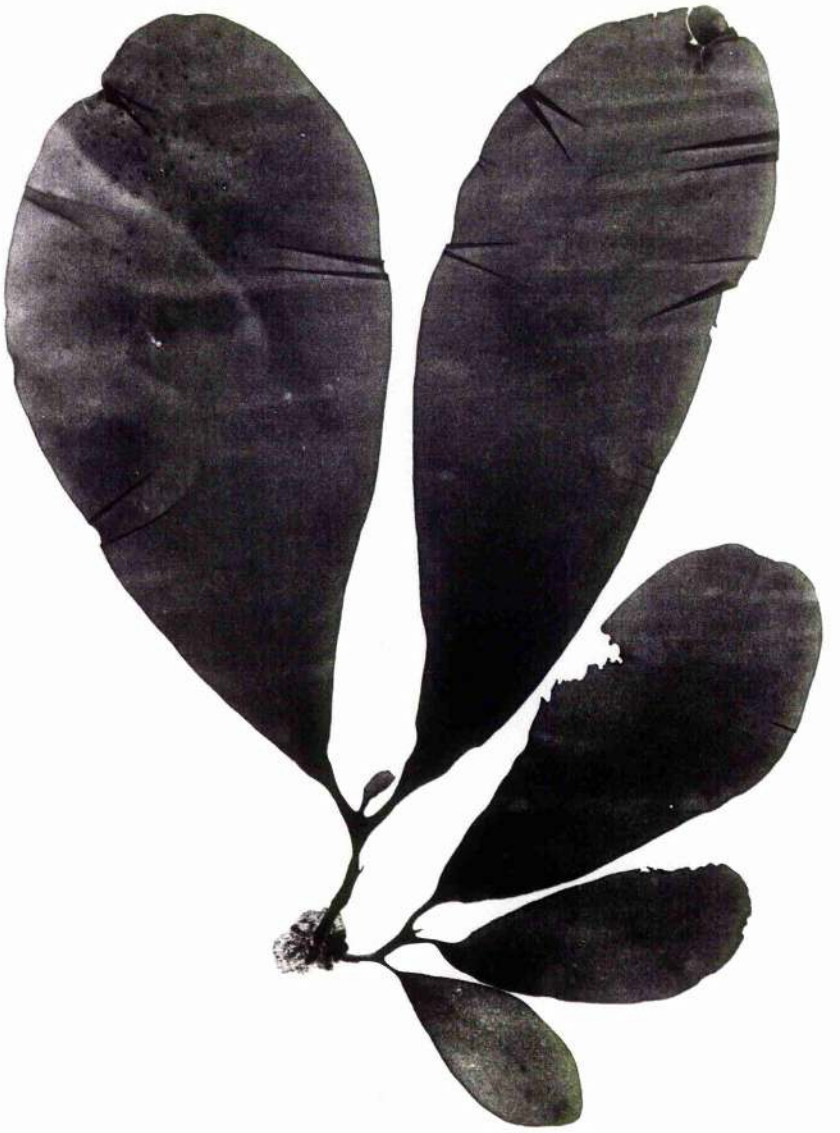


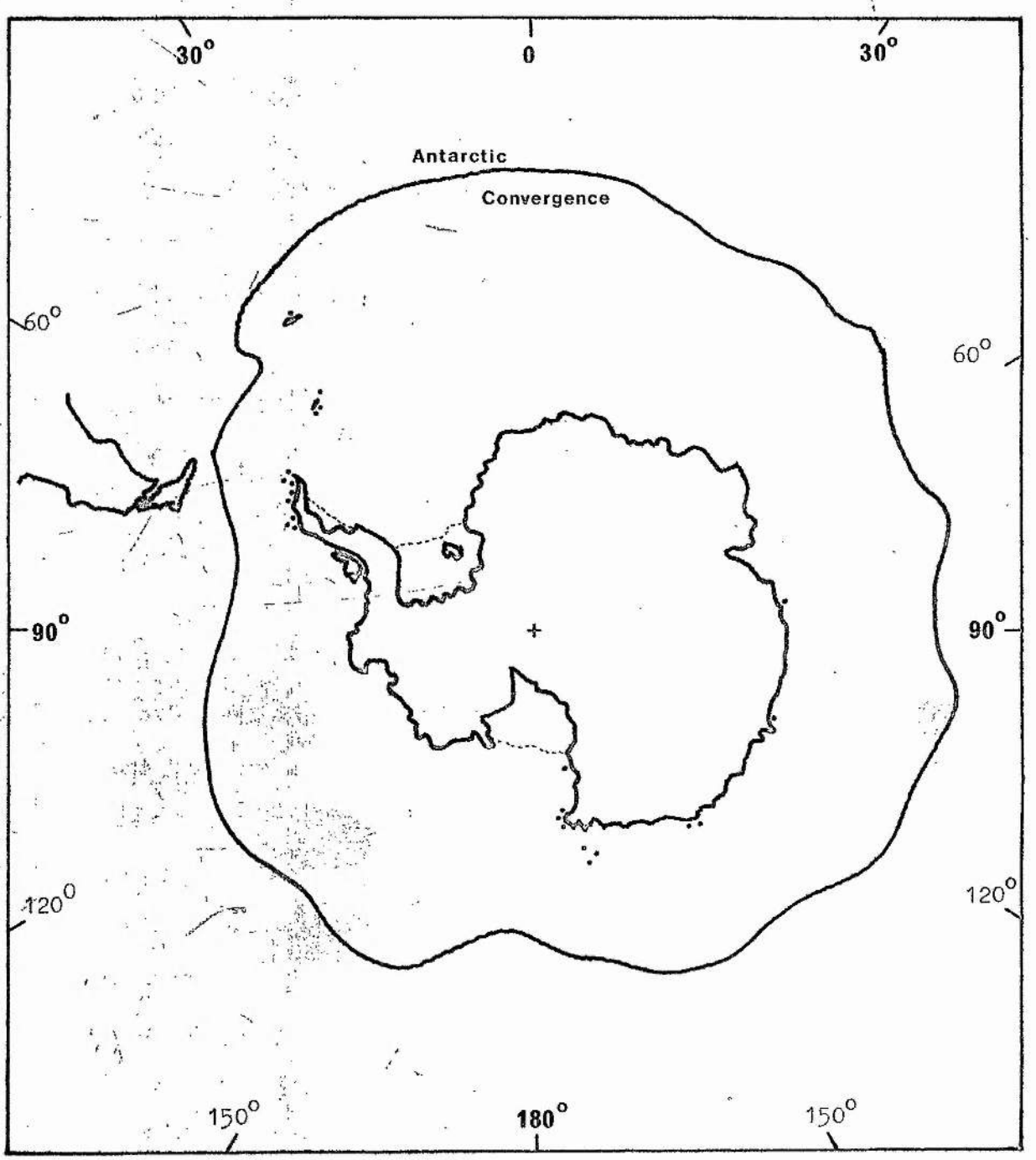
Plate 4 shows the laminae and stipes adopting a spiral form on the sea-floor. While this case is an extreme example such spiralling was commonly seen in the stipes. It may be due to differential growth, i.e. the thinner edges of the lamina or stipe growing in area faster than the thicker centre. Plate 2 gives an impression of the size of a mature lamina as compared with a diver.

Re-examination by Neushul (1962) of a plant thought to be sterile when collected revealed a darker area that proved to be a sorus containing two-celled paraphyses and unilocular sporangia. According to Neushul, the sporangia have a corona-like structure at the apex and contain sixteen discrete nucleated bodies at maturity. The paraphyses have an upper, almost cuboidal cell subtended by a larger rectangular cell. Not all the details described by Neushul are however apparent from his illustrations.

The genus Phyllogigas presents a problem in that its intercalary growth zone and superficial meristem suggest the order Laminariales, whereas the sporangia do not (Neushul, 1962). Papenfuss (1964) states that the systematic position of Phyllogigas is wholly uncertain. This genus and its closely related Antarctic form, Phaeoglossum are distinguished from others in this order by a unique internal assimilation tissue first observed by Gain (1912). The reproductive bodies are also distinctive, being similar to those of the Desmarestiales. The peculiar corona at the apex of the sporangium of Phyllogigas might be interpreted as a ruptured cell, homologous to the upper cubical cell of the paraphysis.

Distribution

Phyllogigas, the largest Antarctic seaweed known, is circumpolar in distribution and a characteristic and not uncommon species in the



Map 4. Circumpolar distribution of Phyllogigas grandifolius (.) (after Zaneveld 1968).

sub-littoral. The largest individual reported had a blade 8m (26ft) long (A. and E.S. Gepp, 1907), dredged in 33m (107ft). The maximum depth to which it descends may exceed 20m (65ft) and perhaps reach 30m (98ft) but higher figures are questionable even if there is no reason to doubt the correctness of the sounding, the dredge can have passed over stretches of lesser depth, (Skottsberg and Neushul, 1960). Samples in this study were collected using SCUBA at over 32m. Dredges have been used because the traditional methods of studying the marine biology of a coast-line-intertidal collecting - are not longer practicable because continuous abrasion by floating ice scours that zone clean. Further difficulties are encountered in areas where fast ice extends out directly into the water, leaving no intertidal zone exposed. The ice often carries away seaweeds, dropping them in deeper water, a possible explanation of 'elittoral' records. Zaneveld (1968) in a very painstaking study, records Phyllogigas at depths of below 300m (980ft) and also records the collection by SCUBA divers of fresh fractifying specimens from under ice during the austral winter of 1967. Map 4 shows the distribution of this species in the Southern Ocean.

The present study of Phyllogigas is part of a detailed long-term investigation of the ecology of Borge Bay involving taxonomy, energetics and population studies of the biota found there, a fairly typical area of inshore Antarctic Sea. The base itself was sited on Borge Bay following the recommendations of a senior British ecologist, Professor J.B. Cragg.

II THE ENVIRONMENT

Introduction

The South Orkneys, a small and compact group of islands lie

some 700km (about 440 miles) east and slightly north of the tip of the Antarctic Peninsula. Despite their northerly situation, they are no warmer than other islands further south, e.g., the South Shetlands because the cold Weddell Sea Current brings fast ice or pack ice to them between March to January each year.

Coronation and Laurie Islands, largest of the group, are heavily burdened with permanent ice-caps, while Signy Island, much smaller, and lying in their lee, has lost all but a remnant of the ice cap that once covered it. Islands such as South Georgia, lying north of the winter limit of pack ice, receive the full benefit of open water throughout the year; the winters there are much milder with temperatures seldom dropping far below freezing point.

The physical features

1. Meteorology

The passage of depressions from west to east to the south of Signy Island produces a prevalence of west and north-west winds. The British Antarctic Survey station is situated on the east side of the island, on a small, north-facing cove (Factory Cove) opening into a larger bay (Borge Bay). Its position ensures shelter from the main force of the prevailing winds by the plateau of the island itself. Winds from the east and south east are fairly frequent so that wave action in the littoral and immediate sub-littoral may occasionally be quite severe. In addition there are frequent warm northerly winds resulting from föhn effects created by the 1,000 - 1,200m (3,250 - 3,900ft) mountain barrier of central Coronation Island. Frequent heavy cloud cover and lack of sunshine are typical features of the climate and give the high occurrence

of precipitation.

The annual temperature regime is typical of Antarctic maritime areas. During the summer months (December - April) the mean air temperature is at or a little above freezing point while during the coldest part of the year (July - September) values of -10° to -12°C are usual. Extreme temperatures during the year may range from $+10^{\circ}$C to below -30°C. Water temperatures rarely exceed $+2^{\circ}$C during the summer and fall to -1.9°C during the winter.

The formation of fast ice and the presence of pack ice around Signy Island are very variable. Fast ice, i.e., sea ice which is frozen fast to the land, usually persists for 5 to 6 months of the year, often from May-June to October-November but both this and the incidence of pack ice are influenced by climatic conditions in the Weddell Sea. The presence of an ice foot, the thick ice left frozen to the shore when the fast ice has broken away, on shore freezing, and the scouring effect of sea ice, all combine to have a profound effect on the littoral flora and fauna.

2. Sea Ice and Temperature

During the winter months sea ice produces a significant reduction in the severity of the physical conditions in the areas studied in Borge Bay, and in other places where it is present. The extremes of temperature experienced on land (e.g. down to -39°C) do not occur in the sea. Floating ice in fact cools the sea in summer, both by reflecting radiation back into space and using up heat in melting, while acting as an insulating layer in winter.

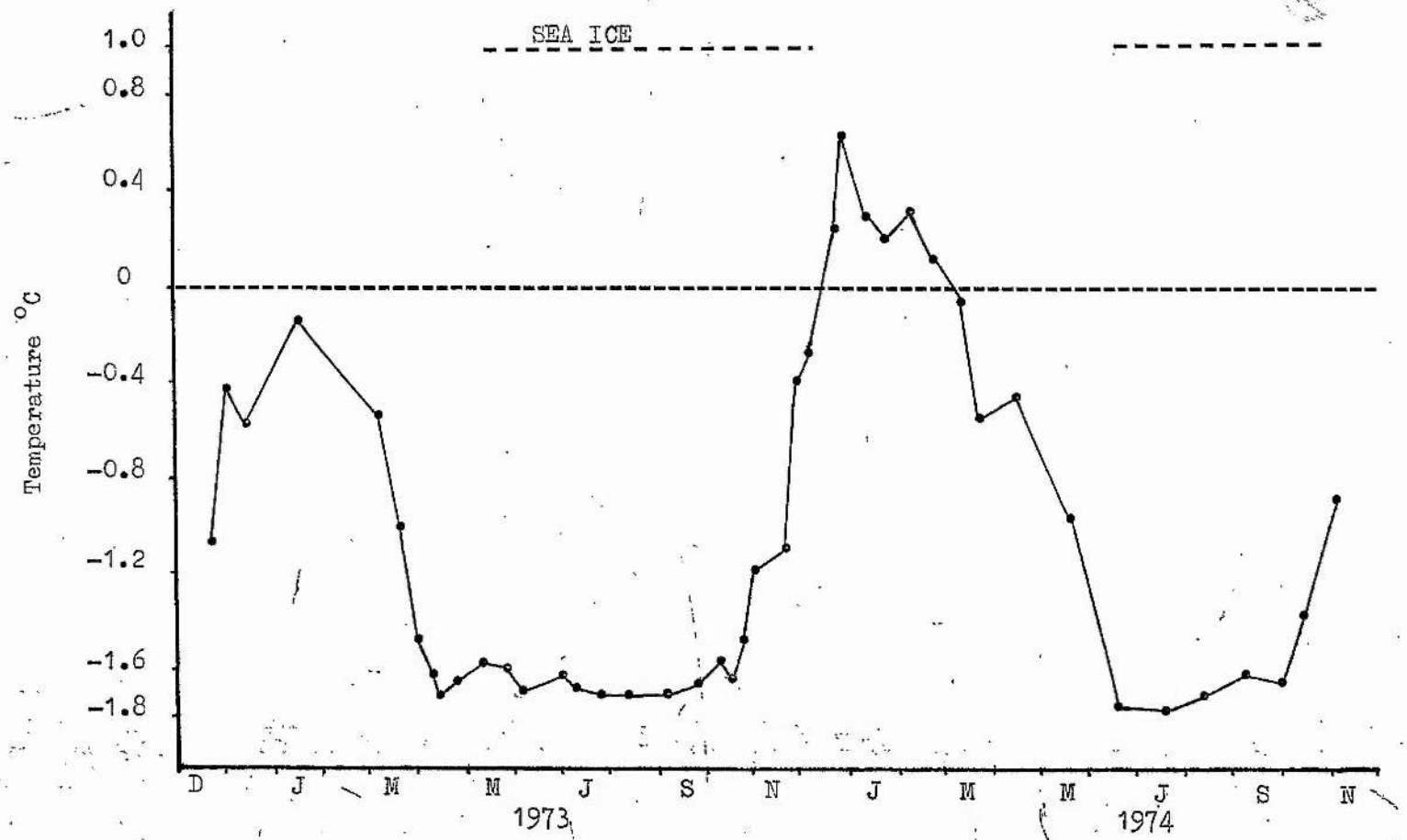


Fig. 2.1 Seasonal variation in temperature at 10m depth in Normanna Strait over 2 years

The effect of the sea ice on the land is much more drastic. Because the ice blankets the sea its presence means that the sea cannot warm the coasts thus producing the long winters of almost continental Antarctic severity: but much warmer summers when the islands are surrounded by loose pack or open water. Though cold, the sea in winter is much warmer than the atmosphere.

Sea water temperatures vary by only 3.5°C between summer and winter, the maximum range being +1.5°C to -2°C. Often the summer sea temperature only reaches +0.5°C. Fig. 2.1 shows sea temperature curves at 10m depth for 1973 and 1974. It will be seen that in 1973 the temperature did not rise above zero at any time, but in 1974 positive temperatures were recorded for 2½ months, mid-January to the end of March, and again during December. The duration of the sea ice is shown and clearly correlates closely with the periods of lowest temperatures (May to December in 1973 and July to November in 1974).

It appears unlikely that the sea ice has any direct physical effect on sub-littoral habitats such as those studied in this work. Obviously the scouring effects of ice will be most severe in the littoral zone but at a site such as Cam Rock locally severe scouring is only produced by grounded ice-bergs and bergy bits (smaller pieces broken away from ice-bergs). This generally does not occur often enough to produce great habitat changes.

Ice cover in Borge Bay is very variable. In most years fast ice (sea ice frozen fast to the land) is present from late May to early October. Occasionally it may break out and refreeze again but a period as long as May to December with unbroken sea ice, as happened in 1973 is exceptional. After the fast ice has broken out, there is a period of

three months when pack ice can be expected. Rarely is this solid and then only for two or three days at the most. According to Bone (1972) ice thickness rarely exceeds 0.5m, though in the seasons covered in this project, thicknesses of over 1m were recorded. These figures do not include pack ice where floes are frequently greater than 2m thick.

Over the vast areas covered by sea ice the thickness is highly variable, ranging from a few cms. on refreezing leads to several metres in the vicinity of pressure ridges or areas of rafting. In a relatively sheltered area like Borge Bay the ice is more homogenous in nature as the conditions leading to its formation do not vary over the bay area.

3. The Light Climate

(a) Under Ice

The factor most influencing the amount of light penetrating the ice is the nature of the ice surface. This may be overlain by snow of varying thickness, drained or saturated with melt water. Within the ice, light attenuation is also influenced by variations in the amount of entrapped brine which gradually drains out during the season (Davis & Munis, 1973), air bubble density (Jaffe, 1960) and grain size (Weller, 1969). However, in the relatively homogenous first-year ice these conditions produce small variations is comparison with overall thickness and surface state. Such variables are difficult to simulate in the laboratory and the complexity of the radiation field beneath the ice has been demonstrated by Clasby et al. (1972) and Bunt & Lee (1970) who worked on seasonal ice and English (1961) and Smith (1973) who worked on perennial ice. Further complications are introduced by algae and diatoms growing on the undersurface of the ice. Bunt (1963), Bunt & Wood (1963)

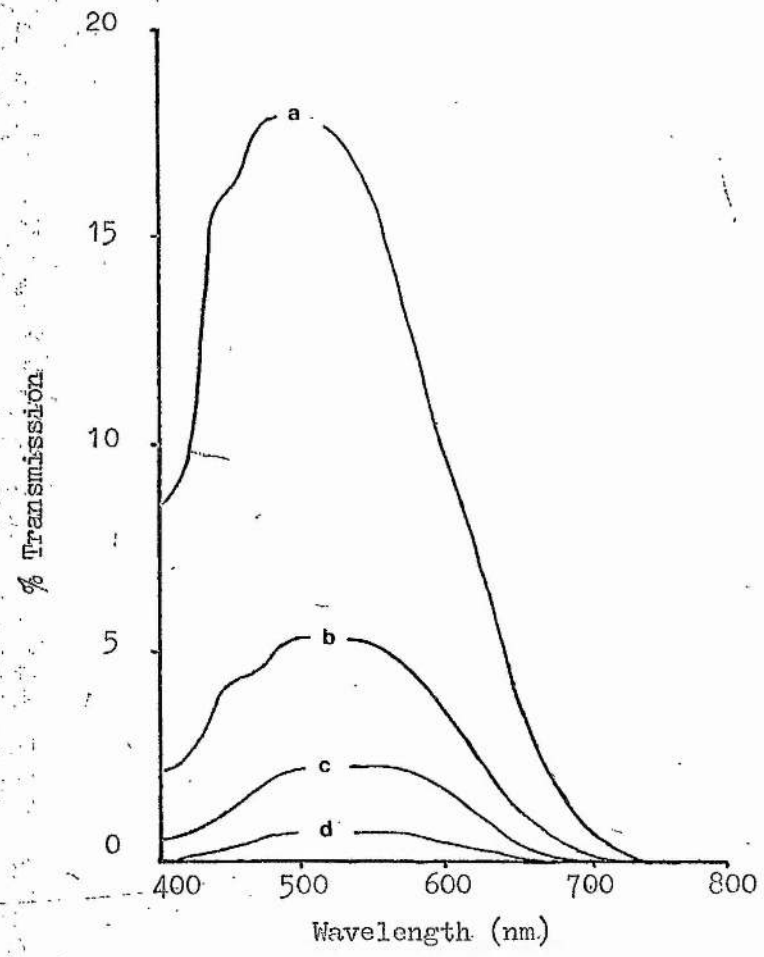


Fig. 2.2 Percentage of incident radiation transmitted by a 185 cms thick slab of first-year sea ice for the four surface conditions described in Table 2.1 (After Maykut & Grenfell 1975).

Maximum percentage transmission for melt pond/blue ice (curve a) was between 490 and 500mm and for the white ice (curve b) at 510mm. For the snow covered ice (curves c & d) on the other hand, the peak transmission was in the green/yellow part of the spectrum at 550mm. This strongly suggests the possibility of selective absorption by foreign material within the ice.

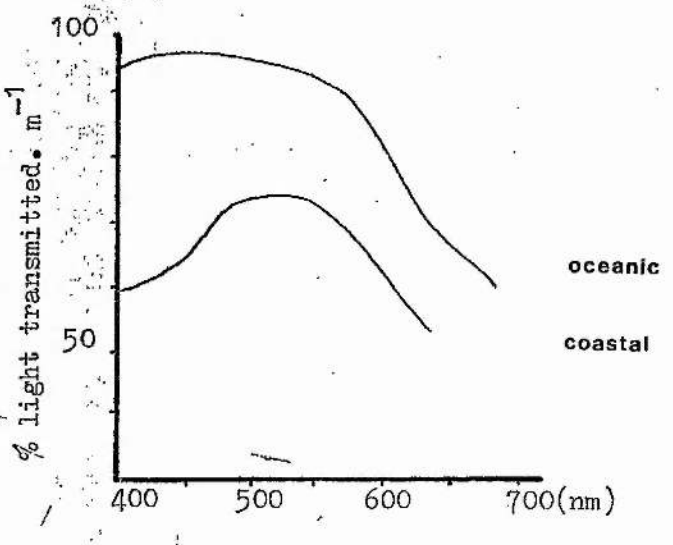
and Bunt & Lee (1970) reported considerable growth in the brash layer below the 1-2m thick cover of sea ice in McMurdo Sound on the continental mainland of Antarctica. Similar observations have been made by Apollonio (1961) in the Arctic Ocean.

Maykut & Grenfell (1975) studied the spectral composition of light beneath first-year sea ice in the Arctic Ocean. They found that the amount of energy transmitted by the ice was largely determined by the nature of the upper surface. They made a detailed study of the light regimes existing under a slab of first-year ice 185 cm thick for a variety of surface conditions and obtained the following results of percentage incident radiation transmitted.

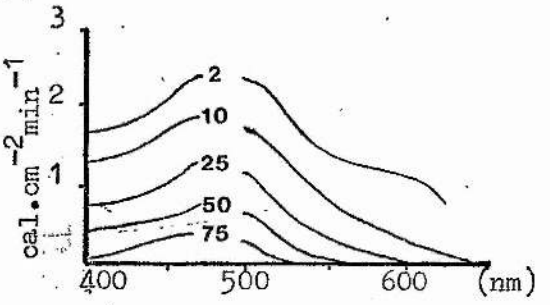
	Nature of Surface	% incident radiation transmitted
a.	Blue ice covered by 5cm deep melt pond	7.41
b.	White ice	2.25
c.	Blue ice covered by 12cm melting snow	1.12
d.	Blue ice covered by 25cm melting snow	0.22

Table 2.1 The relation between different ice surfaces and percentage incident radiation transmitted

Comparison of these figures for percentage transmission show that melt pond ice transmitted about 3.3 times as much energy as the adjacent white ice which in turn transmitted an order of magnitude more energy than ice covered by 25cm snow. The spectral distribution of this radiation is shown in Fig. 2.2.



a)



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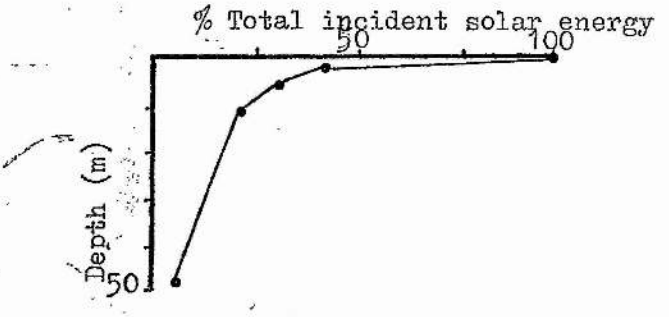

c)

Fig. 2.3 a) Penetration of different wavelengths in different sea water samples, b) spectral distribution of radiant energy at different depths, c) changes with depth of % total incident solar energy. ((a) after Sverdrup, Johnson & Fleming (1942), (b), (c) after Jerlov. (1964)).

(b) Surface Insolation

Light falling on the sea continually changes its spectral composition and also shows changes in intensity with different sky conditions. Surface reflection accounts for about 4% of incident radiation on a calm day and 25% on a day with a moderate wind producing waves and a swell. The light that penetrates the sea decreases in intensity with depth (Fig. 2.3c) for several reasons:-

i) Absorption by water molecules

ii) Absorption by dissolved matter and suspended particles

iii) Scattering by suspended particles

The rate of absorption is greatest in the surface layers: the amount of scattering being obviously dependant on the amount of suspended matter. Hence where there is appreciable turbidity, the deep underwater illumination will be of predominantly green light (Fig. 2.3(b)).

Turbidity around Signy Island may be caused by run-off from the land and melt-water from the glaciers. A layer of diatoms has been observed on the undersurface of the sea ice, and as this melts and breaks out, the diatoms settle very slowly through the water column. Run-off will be greatest in early summer, during the period of maximum day-length. Fig. 2.4 shows how day-length varies during the year, from a minimum on June 21st of 5.5 hours to a maximum on December 21st of 19.2 hours. This curve should be compared with Fig. 2.5, a histogram showing the monthly incident radiation levels for Signy Island in kcal.cm^{-2}. It will be seen that in two of the three years considered 1972 and 1973, November had the same or more incident radiation than December, despite a shorter day-length. The totals for the three years considered are given in the table overleaf.

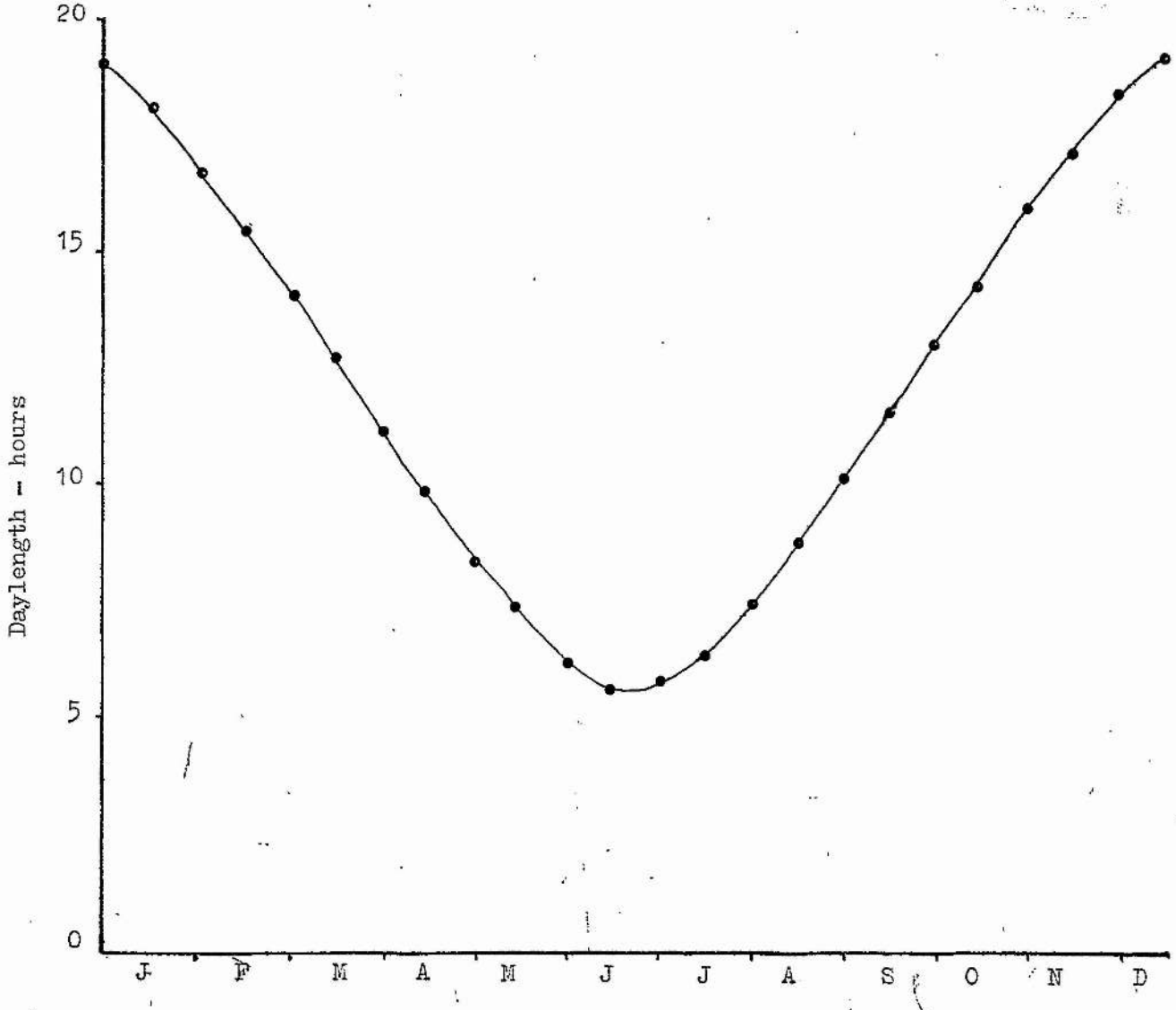

Fig. 2.4. Seasonal variation in daylength, Lat. 60°S

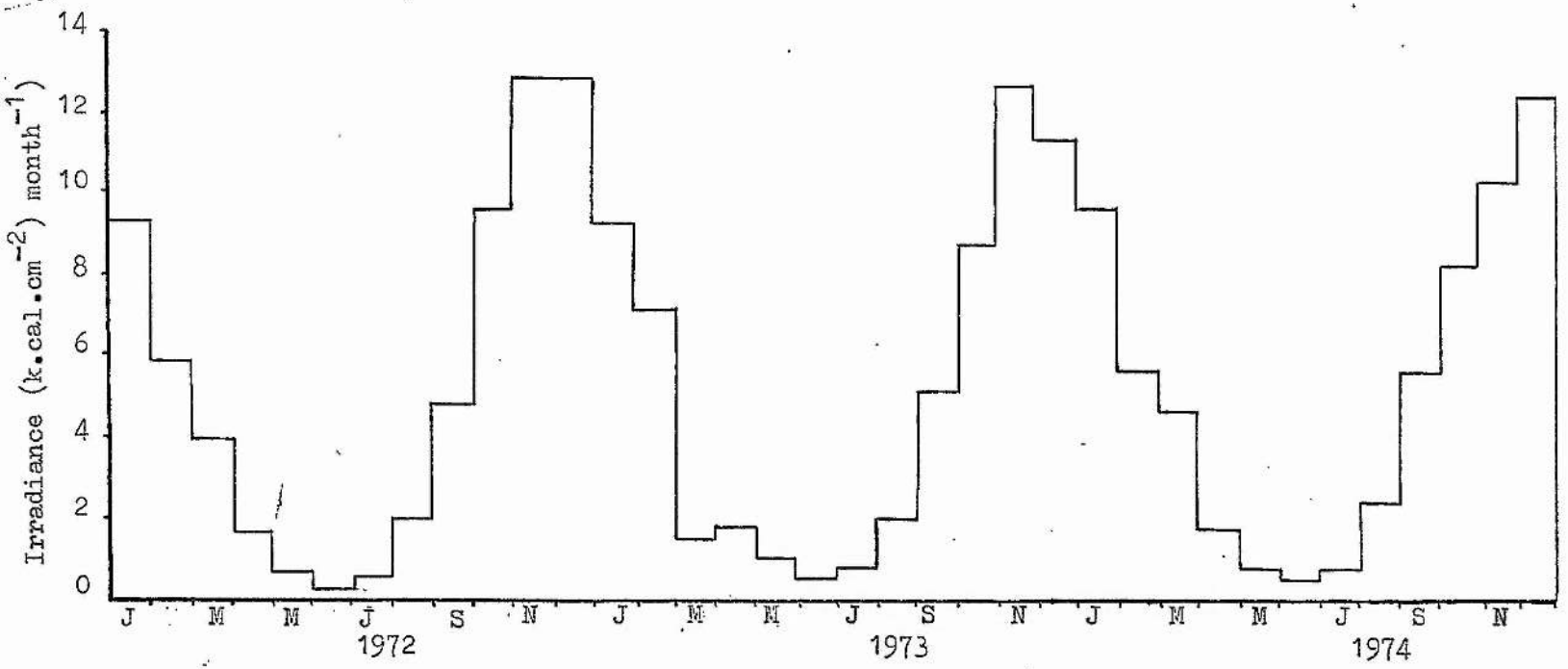

Fig. 2.5 A histogram showing monthly incident surface irradiance at Signy Island, Lat. 60°S in k.cal.cm^{-2} over a period of 3 years.

1972		1973		1974	
kcal/cm^2	W/cm^2	kcal/cm^2	W/cm^2	kcal/cm^2	W/cm^2
63.95	4661.61	60.32	4214.57	59.73	4338.38

Table 2.2 Total incident radiation for three years at Signy Island; lat. 60° 41'S

For the latitude of 60°S the maximum possible radiation in a transparent atmosphere should be ca:

Gates (1962) 34 kcal.cm^{-2} for winter
149 kcal.cm^{-2} for summer
183 kcal.cm^{-2} for whole year

Signy Island receives considerably less than these theoretical maximum figures; in only one of the three years considered does the incident radiation reach even one third of the maximum possible. This is due to the heavy mist and cloud cover produced by mixing of the cold Weddell Sea Current, or East Wind Drift (Knox, 1960), with the (relatively) warmer waters of the circumpolar West Wind Drift, to the north-west of the South Orkneys group. For detailed accounts of the hydrology of the Southern Ocean see Deacon (1933, 1937) and Knox (1960).

Figs. 2.6a and 2.6b show the percentage of the incident radiation at the surface reaching depths of 5 and 10m respectively, approximately the depths of the two sites. Readings were taken over several seasons; those shown here being for 1973. The effect of the sea ice is immediately apparent. High light levels were observed in April (Autumn) as the phytoplankton bloom (see next section) sometimes associated with this season is very small (0.72 ug Chl a.l^{-1} on 9.4.74 at 6m rising to a maximum of 1.83 ug Chl a.l^{-1}

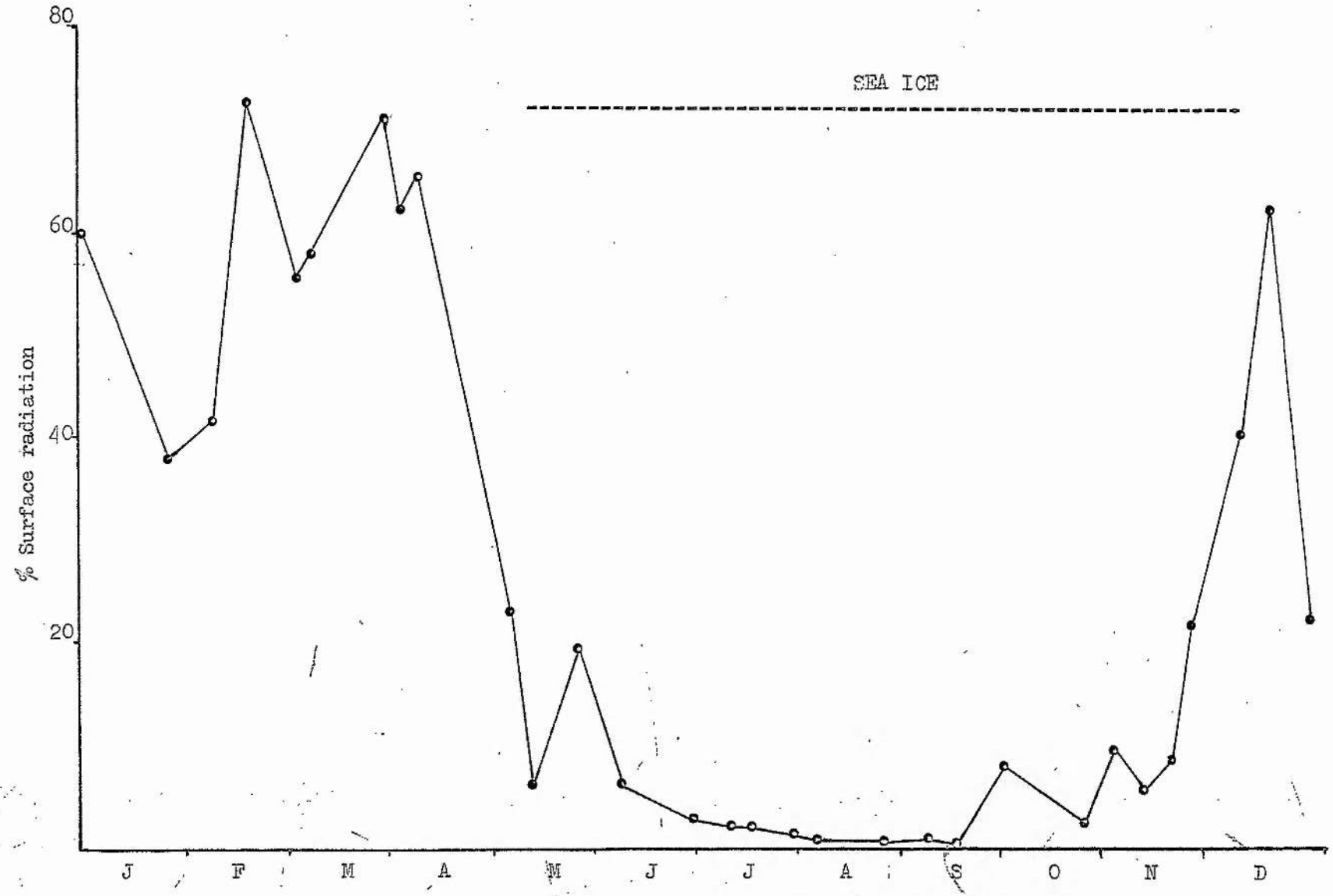

Fig. 2.6a Seasonal variation of Incident Radiation at 5m depth expressed as % surface radiation over 12 months with duration of sea ice shown at top of each graph.

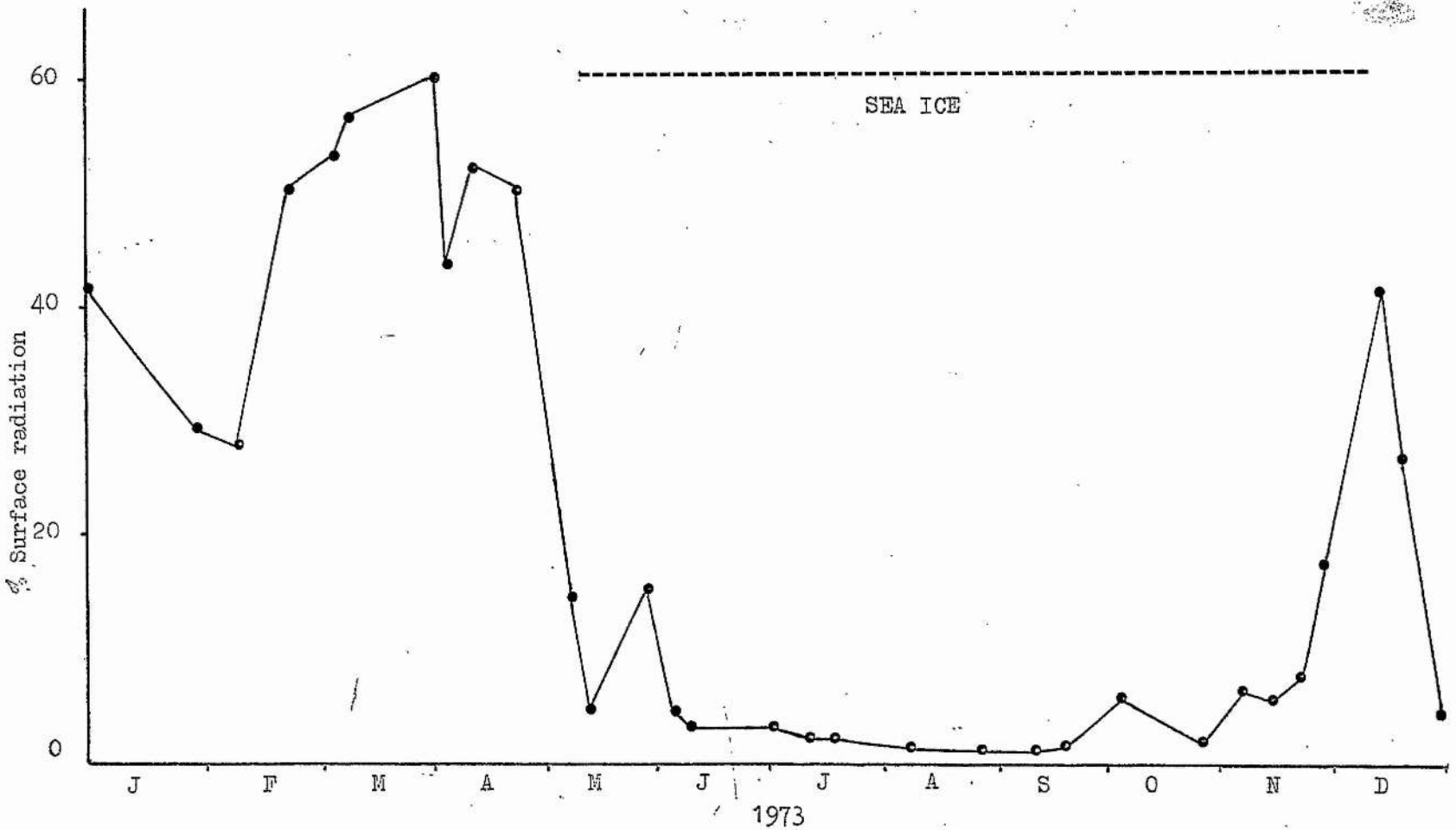

Fig. 2.6a Seasonal variation of Incident Radiation at 10m depth expressed as % surface radiation

on 15.4.74 and then decreasing rapidly to nearly zero). These light levels were rapidly reduced as the daylength continued to decline and the sea surface began to form a layer of ice, further reducing the light levels. The ice ultimately reached a thickness of over 1m. This lasted until the first week in December, thinning noticeably after August but without a significant increase in light levels. Once the ice had broken out, there was a rapid increase and a surge of growth in both the phytoplankton and Phyllogigas was observed.

Increasing phytoplankton density will reduce the light reaching the attached algae, thus reducing their photosynthetic activity. The lower limit at which phytoplankton can grow in the ocean is the depth to which only 1% (Steemann-Nielsen, 1975) of light penetrates. At Signy Island in December 1972 this depth was below 200m and fell to 5m during August and September (winter) 1973. Seaweeds growing on the bottom can extend a little further to depths where the light intensity is less than 0.3% of the surface value (King, 1975), though the depth at which this level occurs is influenced by several other factors e.g., the amount of suspended matter in the water column of which phytoplankton can make up a considerable part at certain times of the year.

THE BIOLOGICAL FEATURES

1. The phytoplankton bloom, and its effect on light and nutrients

The most widely used method of estimating phytoplankton productivity is to determine the concentration of photosynthetic pigment (usually chlorophyll 'a') in a known volume of sea-water, as described by Strickland and Parsons (1965). This was the method used in this study.

Temperature, salinity and light are all important environmental

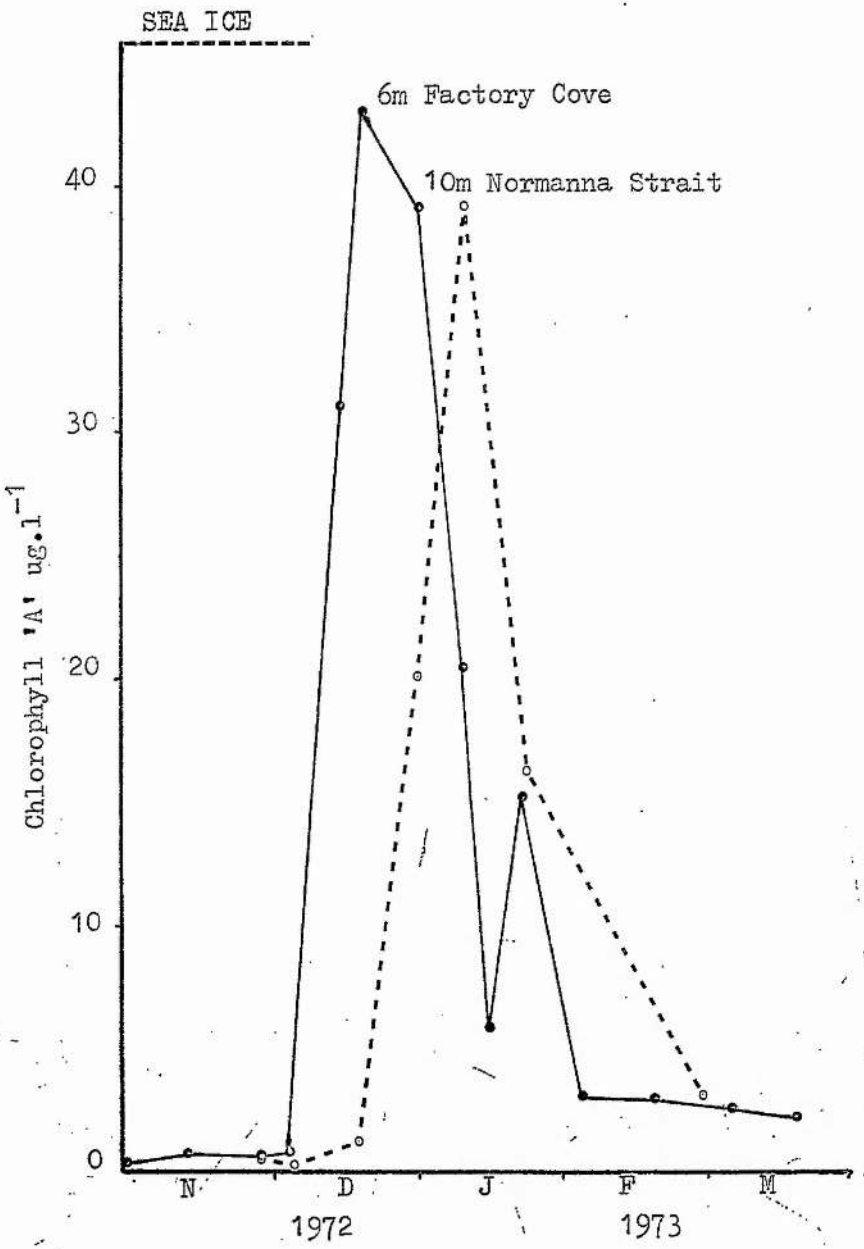

Fig. 2.7 Chlorophyll 'A' concentrations in ug.l^{-1} at similar depths to the sampling sites. Summer 72/73

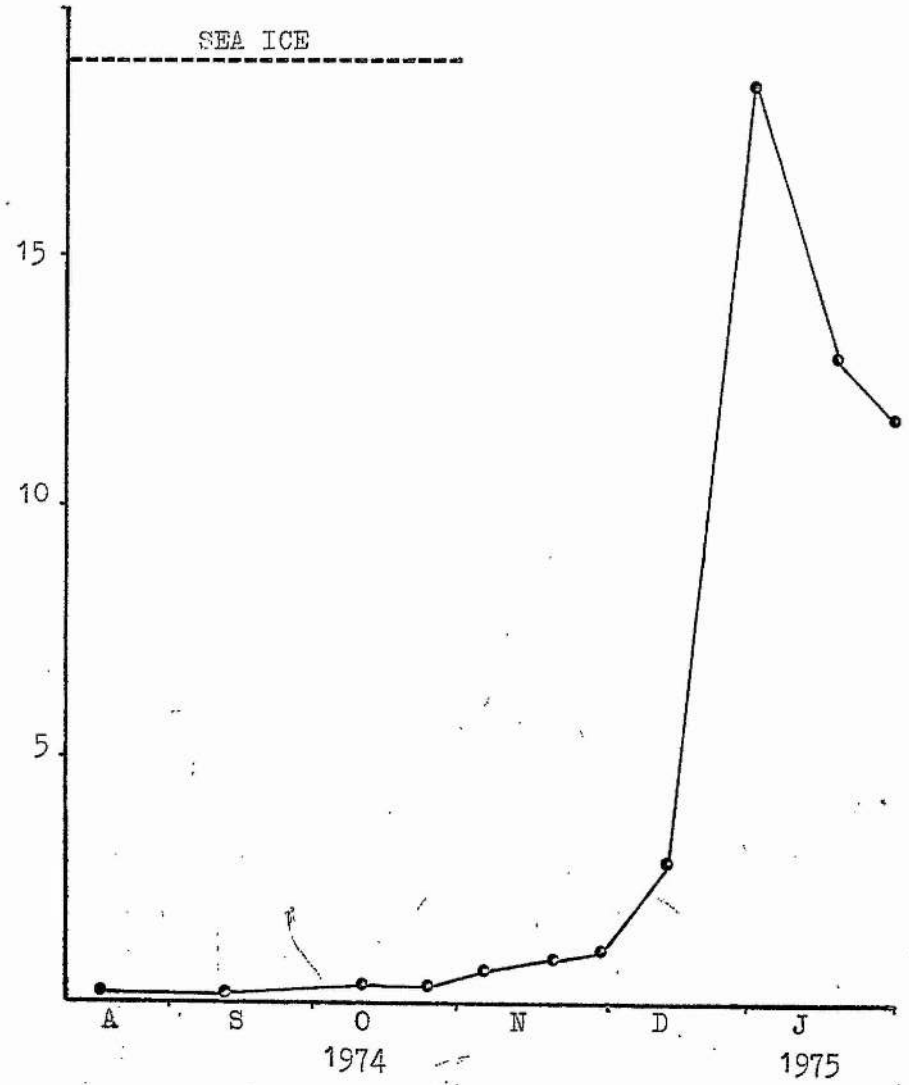

Fig. 2.8 Chlorophyll 'A' concentration in ug.l^{-1} at 6m in Factory Cove. Summer 74/75

factors in macroalgal productivity, acting directly on the algae and indirectly by their influence on the phytoplankton, which when conditions are right, is highly productive. It was thought that these factors, and any others, such as nutrient levels in the sea-water, which influence the growth of the phytoplankton should be assessed to determine their effect on the productivity of Phyllogigas.

Studies on plant nutrient requirements emphasise the importance of nitrogen and phosphorus. The reproductive capacity of the phytoplankton depends to a considerable extent on the availability of nutrients which must be in the uppermost layers, where there is light, to be of any use to the phytoplankton. Thus nutrient supply will indirectly influence the growth of the macro-algal population via the phytoplankton. Availability of nitrogen and phosphorus will help to determine the density of the phytoplankton, which as previously explained, will influence macro-algal photosynthesis. Generally, once the surface supply of nutrients has been used up, the sea will lose its fertility unless the nutrients are replaced. This however, does not happen in the Antarctic Ocean where the nutrient supply is non-limiting (Deacon, 1933).

Figs. 2.7 and 2.8 show how abrupt and short-lived a phenomenon the spring phytoplankton bloom is in this region. Fig. 2.7 covers the period of the bloom in the 1972/73 season, observations being recorded for two depths, one at 6m in Factory Cove, close to the shallow site in the productivity studies and the other at 10m in Normanna Strait. Fig. 2.8 for the sake of clarity shows only the 6m curve for the 1974/75 season. In this case the 10m curve follows that shown almost exactly, although peaking at a slightly higher value, 26.8 ug chlorophyll.l^{-1} on the same day as the 6m curve and dropping as abruptly to merge again with the 6m curve in January.

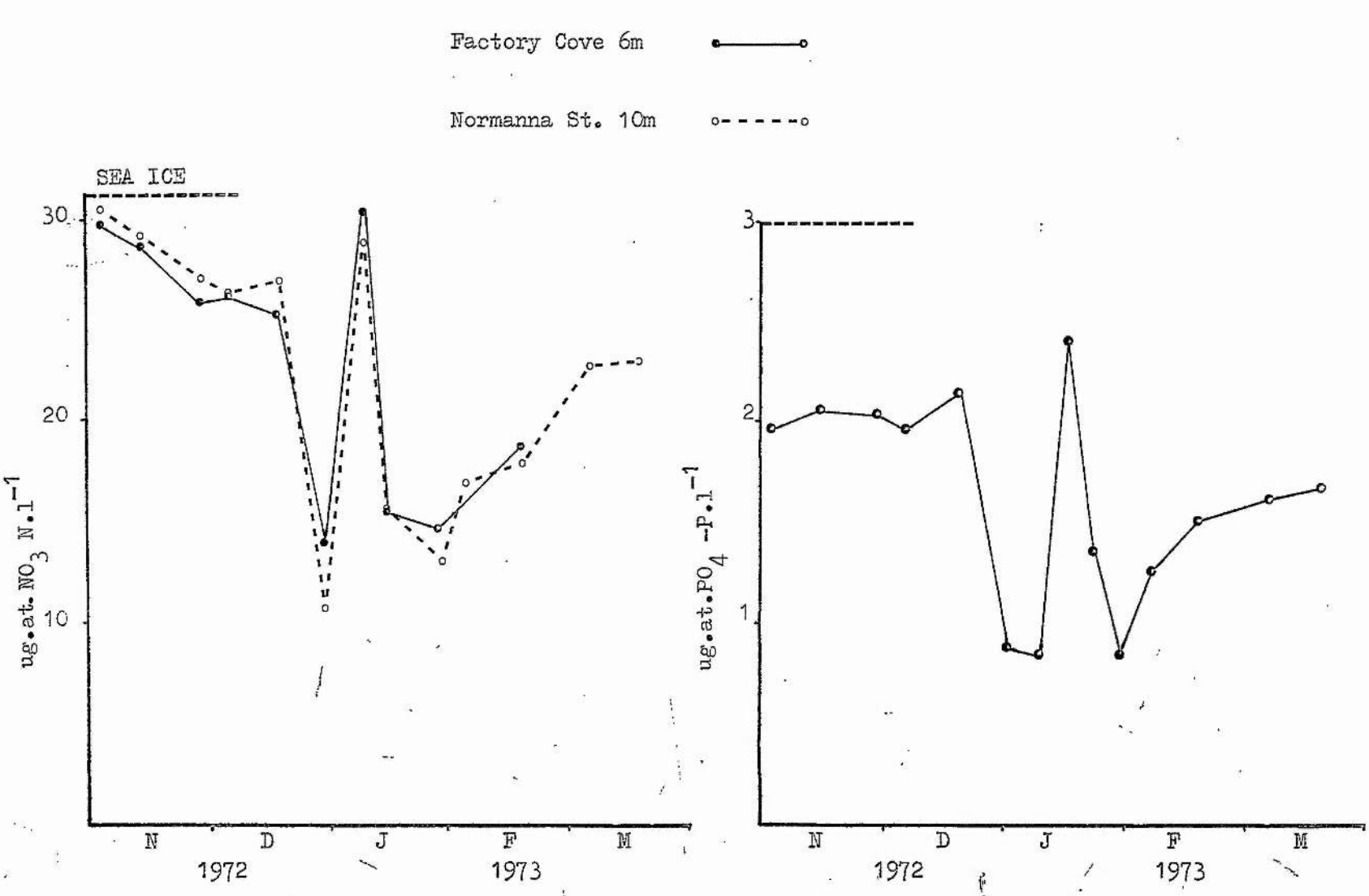

Fig. 2.10 Seasonal variation in nutrients, nitrate -N (left) and phosphate -P (right). in ug.at.l^{-1}. Note differences in scale. Only one phosphate curve drawn for clarity.

Returning to Fig. 2.7 it will be seen that the peak of the bloom at 6m occurred on 18th December 1972 and the peak of the 10m bloom occurred over three weeks later on 9th January 1973. A secondary peak can be seen on the 6m curve on 22nd January.

Over this period (December to January) the incident radiant energy levels (Fig. 2.9) show a very sharp rise as the sea ice broke out on 14th December, producing a maximum level of radiant energy on 18th December.

The incident radiation at 10m was calculated from the expression:

$$\frac{\text{Incident Surface Radiation } (\text{cal.cm}^{-2}\text{day}^{-1})}{\text{Day length (hr)} \quad \text{x} \quad R_{10}} = \text{Incident Radiation at 10m } (\text{cal.cm}^{-2}\text{.hr}^{-1})$$

where R_{10} is that fraction of the surface radiation reaching 10m, calculated directly from light readings made on the spot.

At the same time, in Fig. 2.10, the concentrations of nitrate and phosphate decreased rapidly. Phosphate is only plotted at the 6m level for clarity as, like the nitrate curves, the values obtained at 10m are very similar to those at 6m. The prominent peaks observed in both nitrate and phosphate curves in the 1972/73 season but not in the 1974/75 season (see Fig. 2.11) are correlated with the secondary peak observed in chlorophyll 'a' levels on the 6m curve. This is probably explained by stormy weather causing a mixing of water masses and an increase in nutrients in the 'new' water. The prevailing turbulent conditions prevented sampling in the more exposed Normanna Strait station as can be seen from Fig. 2.7 when all the sampling in February and March 1973 was confined to the relatively sheltered waters of Factory Cove, otherwise a further secondary peak might have been observed.

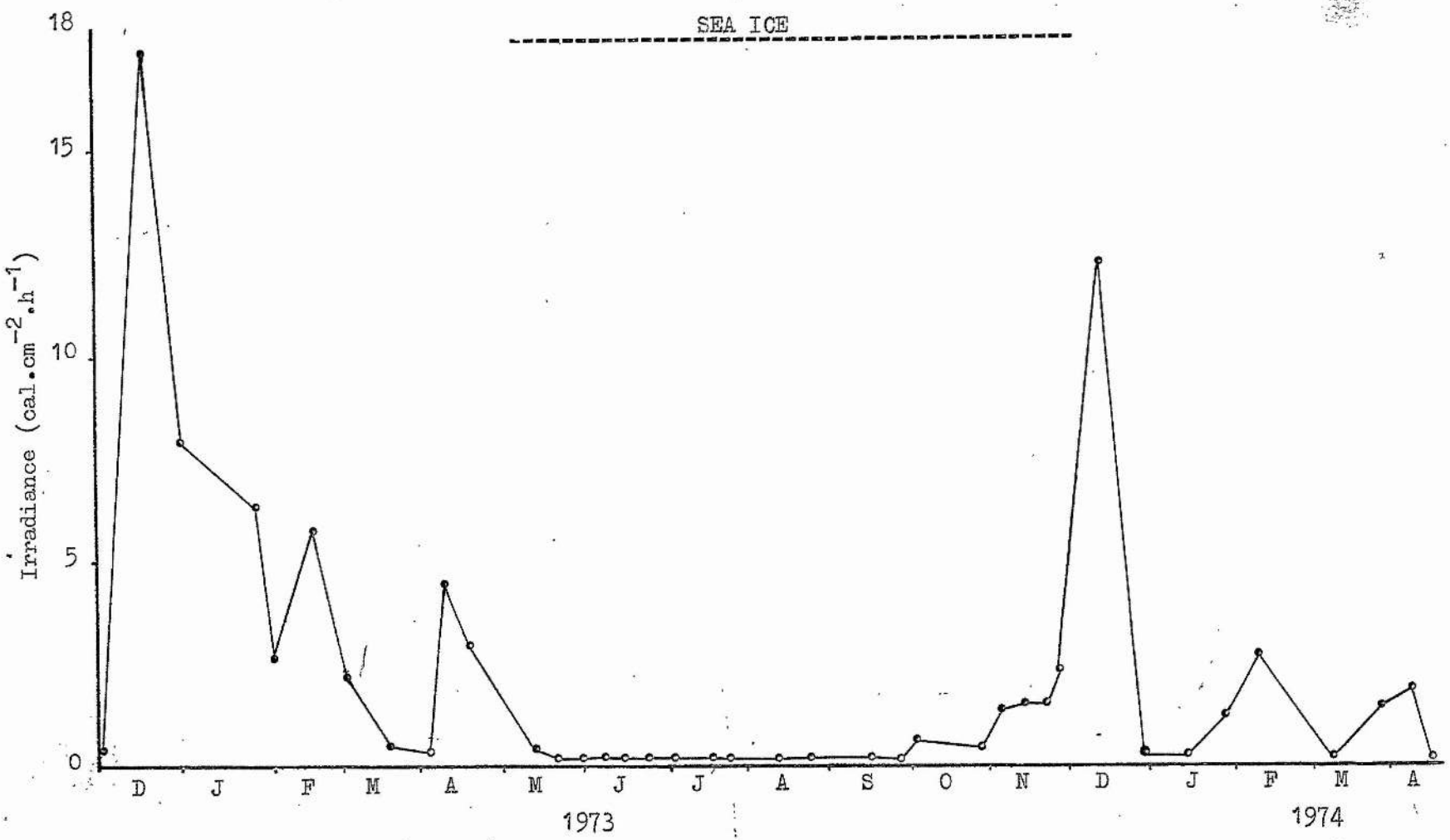

Fig. 2.9 Seasonal variation in irradiance at 10m depth over a period of 17 months

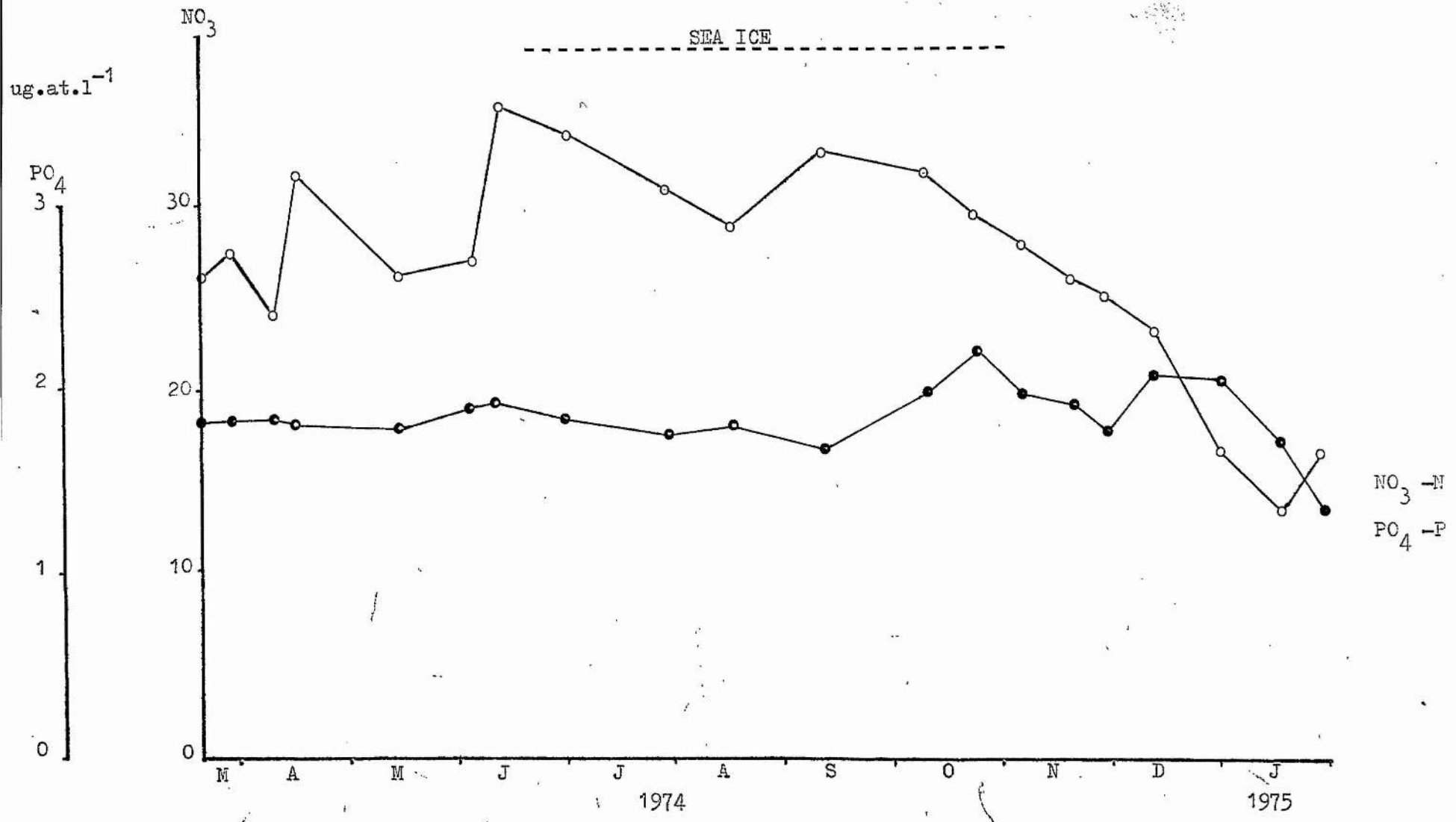

Fig. 2.11 Concentration of nitrate and phosphate at 6m in Factory Cove during 1974/75 season. Units are ug.at.l^{-1}. Note scale differences.

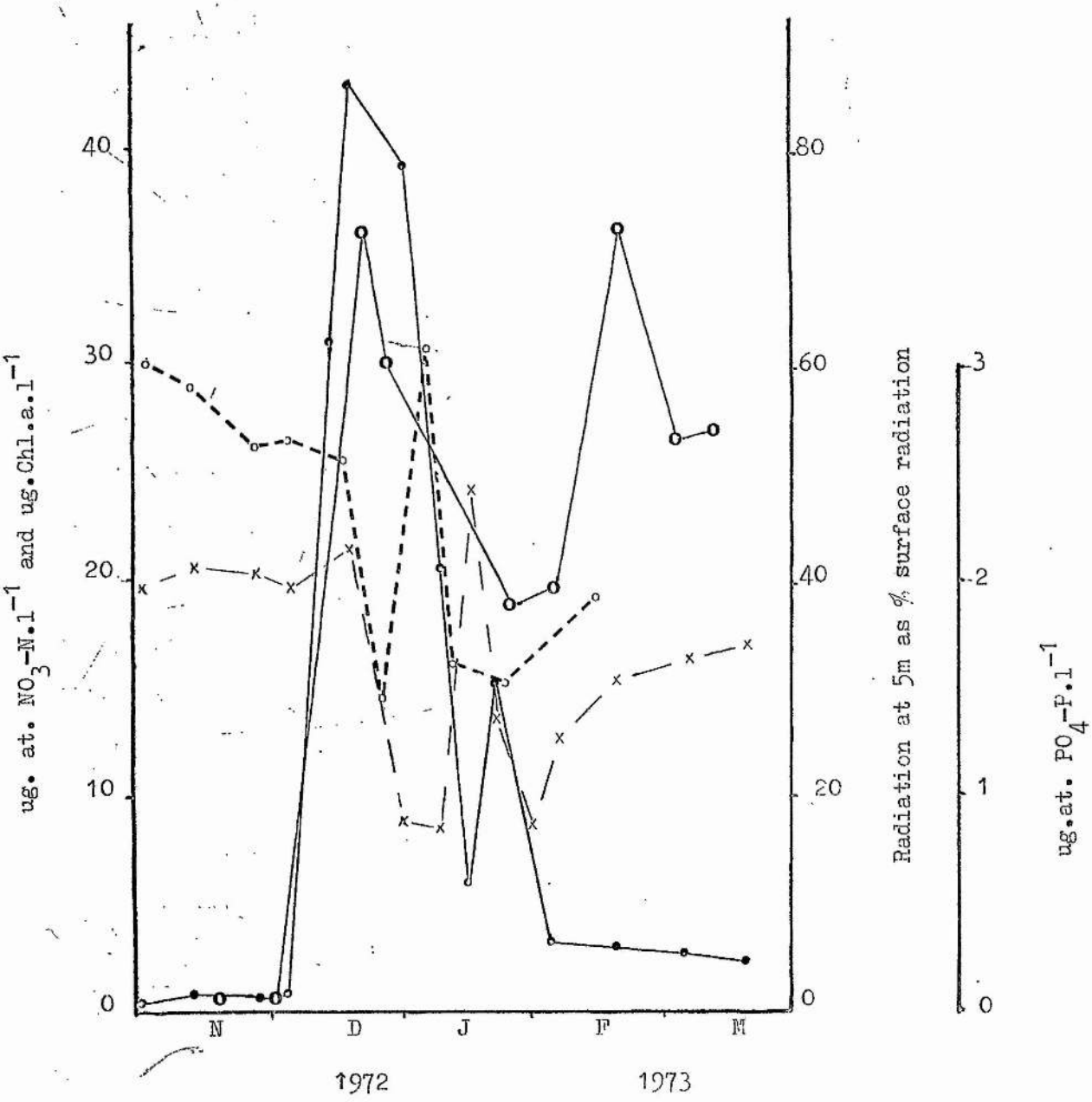

Fig. 2.12 Fluctuations in summer levels of nutrients (PO_4-P and NO_3-N) Chlorophyll 'a' at 6m in Factory Cove, and light at 5m.

KEY

x — x ug.at PO_4-P. l^{-1}

o - - - o ug.at NO_3-N. l^{-1}

●——● chl. a ug. l^{-1}

o——o Radiation at 5m as % surface radiation

Doty (1971) has recently discussed the importance of water turbulence and diffusion for the growth of algal populations in the sea. He points out that more turbulence leads to more diffusion and hence to more nutrient uptake and growth. It would appear that with increased turbulence the current and diffusion boundary layer thicknesses were decreased in the tropical populations he studied. For a detailed account of phytoplankton periodicity see Hart (1942).

The peaks on the nitrate and phosphate graphs occurred on 10th January and declined over the same time period as the chlorophyll 'a' concentration rose; about one week. At the same time the light levels were also dropping (see above) and from the beginning of February the chlorophyll 'a' concentration had dropped to about 3ug.-at.l^{-1} compared with 43ug.-at.l^{-1} at the peak of the bloom. From the beginning of February onwards the nitrate and phosphate levels began to rise once again. See Fig. 2.11 for examples of winter levels.

Fig. 2.11 shows the nitrate level beginning to decline rapidly at the beginning of December and the phosphate at the beginning of January. The light levels rise to a maximum in December with the break-out of the sea ice, as previously described for Fig. 2.9, and fall to very low levels for the first half of January when the chlorophyll 'a' concentration is just declining from its peak value (see Fig. 2.8). The nitrate and phosphate reach their minimum values at the middle and end of January respectively by which time the chlorophyll 'a' concentration is falling rapidly, towards winter levels once again. For comparison see Fig. 2.12 opposite.

THE SHORE AND SHALLOW WATER ENVIRONMENT

During spring and summer when the terrestrial snow cover is melting large quantities of fresh water run into the sea. Sudden thaws may occur during the winter months, e.g. September 1974, when the sea ice is still present. This water, which may also be of a higher temperature than the sea water, does not readily mix with it and during periods of warm weather

the run off can form a surface layer of water with a very low salinity over extensive areas of Borge Bay. As with the ice-scour, the effects are felt most strongly by the shore communities.

Further changes may be brought about more directly by the weather. Strong sunlight, shining on dark rocks in shallow water may raise the temperature by 2 to 4C°, temperatures up to +4°C being recorded in pools on the shores of Borge Bay. Similarly very cold winds will rapidly cool shallow waters and form ice on the shore. The tides ensure that exposure to these 'extreme' conditions are of short duration only.

During ice formation the entire shore and shallow waters may be clogged with ice and are thus very inhospitable. When the sea ice reaches maturity the floating ice is connected to the solid ice foot by a series of blocks, floating up and down and tilting with the tide. Observations by divers at break-out suggest that the shallow sub-littoral zone is relatively undisturbed. Anchor ice may form extensively in this area. It appears during very cold spells as large platelets of ice growing on the sea bed down to depths of about 33m. Slight currents may lift huge pieces of anchor ice, often 40cms thick, which float up to the surface carrying algae, starfish, etc., with them.

MARINE FLORA AND FAUNA

A wide variety of littoral conditions are found in Borge Bay area (Map 3). Rocky shores may be steeply inclined or nearly flat and the rock is either smooth or heavily dissected. Pools of various sizes occur during the summer months. The very irregular local topography results in widely differing degrees of insolation and wave action on various shores. In general, the west coast is far more exposed to wave action than the east; the prevailing winds and currents coming from the west. Boulder beaches occur in a number of areas and there are some littoral accumulations of shingle, e.g. Factory Cove. Areas of fine sand and mud with scattered boulders occur in some sheltered localities, particularly at Elephant Flats

(Shallow Bay) where a shallow lagoon is protected from wave action by an old terminal moraine of the Orwell Glacier.

The submarine topography is very irregular. Rock and boulder slopes occur under most shores, extending to a depth of 5-20m (16-65ft.) before being replaced by areas of sand and mud. In inshore areas, these plains of sand and mud are interrupted by rock outcrops, boulders and moraihic deposits. Although bottom deposits are of a mixed nature, there is a tendency for gravels and sands to occur in shallow water close to the shore and silts in deeper water farther offshore.

The environmental factors influencing the life of marine algae will vary according to the type of habitat. The effects of fresh water run-off and ice abrasion for instance, will be felt most in the intertidal region, while seasonal and diurnal fluctuations in air temperature and similar changes in light intensity will influence a far wider range of habitats. This also applies to the effects of water movements, such as waves, tides and turbulence. Intertidal algae appear better adapted to withstand metabolic stress than those from deeper water, which live in a more stable, less rigorous environment.

The following brief account of the flora and fauna of the littoral and sub-littoral is based on a published summary by Price and Redfearn(1968),(taxonomic authorities as quoted in that work) and on additional personal observations by the author.

On rocky shores the flora and fauna are poor both in numbers and species, unless rock pools are present or the substrate is dissected with cracks and crevices, providing protection from ice abrasion. (Ulothrix and Urospora were observed to form a broad band around Factory Cove (summer 1975) at mean high water level. Porphyra is also found at

this level and the limpet Patinigera polaris colonises the shore and may be common during the ice-free periods of the year. Shingle beaches are usually sterile but sand and mud flats support a limited fauna of burrowing organisms.

At low water spring tides (L.W.S.T.) the algae Leptosomia, Lithothamnia and Iridaea occur on rocky substrates and in the immediate sub-littoral, Curdiea is found also. Patinigera occurs at this level and in suitable areas, stands of encrusting organisms (particularly Bryozoa, Porifera and hydroids) provide shelter for annelids, amphipods and nemerteans. At 1-1.5m below L.W.S. the algae Desmarestia menziesii and Ascoseira mirabilis are frequently co-dominants below which Desmarestia anceps extends down to depths of about 9m (29ft). The large bush-like form of D. anceps provides many micro habitats for other organisms. Small epiphytic algae are common, (though not on Phyllogigas). Several species of mollusc (Patinigera, Margarella etc.) crawl on the fronds of D. anceps which provide shelter for large numbers of amphipods such as Atyloella magellanica, Pontogeneia antarctica, Bovallia gigantea and Paradexamine fissicada. The holdfasts of the algae and to a lesser extent, their stipes, support dense growths of sessile organisms (particularly small algae, Bryozoa, Proifera spirorbid Annelida and hydroids). The epiphytes in their turn provide shelter for many small organisms particularly annelids and the amphipods Probolsica ovata, Jassa falcata and Parajassa georgiana. Sponges of the genus Iophon frequently occur in rock crevices in this zone and it is probable that the amphipod Polycheria antarctica is associated with these sponges in the same way that small dexaminids associate with sponges in European waters. Below the level of D. anceps and extending to at least 30m (98ft) the dominant species is Phyllogigas grandifolius. The

associated epiphytes are generally rather more sparse than on D. anceps. Among both P. grandifolius and D. anceps several species of asteroid and the large isopod Glyptonotus antarcticus may be abundant. Several species of notothenиid fish also occur. It should be noted that the zonal bands of algae reported by Price and Redfearn were not at all apparent during 1972-75. As the map of the shallow sampling site shows (see this Chapter), representatives of Rhodophyceae, Phaeophyceae and Chlorophyceae were numerous between 3 and 6m with no evidence of zonal patterns.

Sediment substrates support infaunas consisting mainly of molluscs and annelids, and a number of species of amphipod. The epifauna on these bottoms consists mainly of molluscs, echinoderms, serolid isopods and fish. A map of the distribution of algae in shallow water (6m) is presented overleaf. The techniques involved are described in Chapter 3.

DISTRIBUTION OF ALGAE IN SHALLOW WATER (6m)

The figure overleaf shows the sparse nature of the flora in the neighbourhood of the shallow site in Factory Cove. The brown algae Phyllogigas and Ascoseira have been recorded individually but the red algae have been drawn en masse. The Leaf Area Index of Phyllogigas in this area was very low, 0.0028 $m^2.m^{-2}$. Most of the algae were found in positions affording shelter from the scouring effects of sea ice. The area mapped is best considered in four unequal parts:

1. An area of shingle, small stones and few boulders in in the south west corner.
2. An open boulder slope to the north.
3. A region of sand along the eastern margin of the area.
4. A region of rock outcrops and gullies occupying most of the area mapped.

Fig. 2.13 Large scale map of shallow site showing distribution of algae (contours in metres)

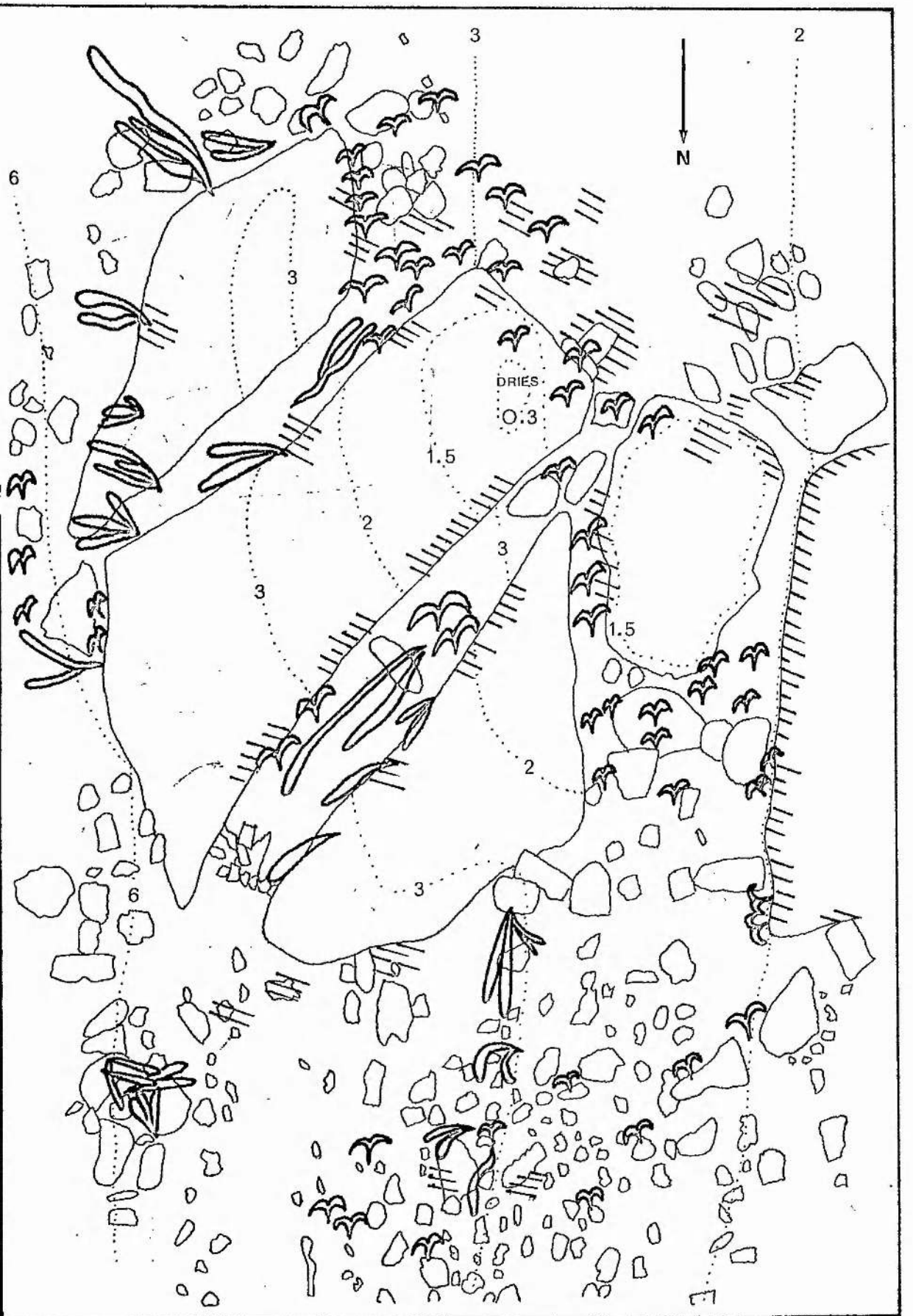

Fig. 2.13 Algal distribution at the shallow site.

Scale 1cm = 1.5m. Depths from Admiralty Chart, 1775, are approximate and are reduced to the level of mean low water of spring tides (MLWS). The distances are taken as measured and not corrected for slope; contours in metres.

Key

Phyllogigas 

Ascoseira 

Desmarestia 

Red algae on all boulders below 2m.

These areas will now be considered in turn.

1. The lack of flora in this area is immediately apparent and is probably due to two main reasons. The area is in very shallow water and thus particularly susceptible to ice scour especially at low tides during the winter months.

The substratum consisted of small pebbles and was relatively unstable.

Most of the plants that are present are confined to the larger boulders or sheltered by the rock outcrops of area 4.

2. Here again the flora is sparse; a few small plants of Phyllogigas and Ascoseira growing in an exposed habitat. Substrate appears to influence distribution here also, the plants being mainly confined to the lower part of the slope where the substrate pebbles are larger.

3. The region of sand extends right across Factory Cove and out into Borge Bay where it gradually gives way to mud and finally bed-rock. The area of boulders and rock is only a very narrow fringe on the slope to the flat cove floor. On the sand no algae were found growing attached to the substrate; the only specimens found were large rafts of detached decaying fronds collected in depressions formed by grounded ice-bergs.

4. This section comprises the greatest part of the mapped area and had the most abundant growth of seaweed though even here it was thinly distributed. The two gullies running diagonally across the area from SW to NE and the wider cleft running north-south contained the majority of the

algae. Red algae were mainly confined to the edges of the outcrops, growing on the vertical rock faces. Most of the algae were found in positions sheltered from ice scour but were often exposed to strong surges, especially in the gullies.

CHAPTER 3

MATERIALS AND METHODS

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CHAPTER 3

MATERIALS AND METHODS

I SOURCE OF ALGA

Phyllogigas grandifolius was collected from two sites in Borge Bay on the east coast of Signy Island. (See Map 3). The shallow site was in sheltered water (6.2m) below low cliffs (approx. 8.0m) in Factory Cove opposite the BAS base. The deep site was farther out in the bay in an area more exposed to easterly swells, at Cam Rock in 10.8m water.

A further site was used once only during winter 1974 at Bernsten Point, immediately to the north of the base, at the entrance to Factory Cove (See Results II).

II REAGENTS

Analar Biochemical or Laboratory Reagent chemicals from British Drug Houses, Poole were used in all cases. C14-labelled sodium bicarbonate was obtained from the Radiochemical Centre, Amersham.

III IN SITU C14 EXPERIMENTS

All diving was carried out from a 14ft. Zodiac inflatable dinghy with an 18 hp. outboard motor, either moored at the site, or in close attendance. (See Appendix 1 for notes on Diving Procedure).

The technique employed is fully described by Drew (1966),

Drew & Larkum (1967) and a modified version for use in British waters by Drew (1972), and Drew et al. (1972). The main advantage of this method is that it permits the measurement of short-term photosynthetic rates of algal tissue under as near natural conditions as possible.

Summary of method

The primary productivity of the alga Phyllogigas grandifolius was measured by the incubation of discs of tissue in Kilner jars containing ^{14}C-labelled sodium bicarbonate in seawater. The uptake of the isotope over the period of the experiment gives a measure of the rate of photosynthesis of the tissue.

By this means it was hoped to determine any seasonal variation in primary productivity; to determine when the maximum rate occurred and to determine the effect of sea-ice on primary productivity during the winter months.

Apparatus

The external morphology of P. grandifolius is very different to that of British Laminariaceae (see Chapter II) thus necessitating some modifications to the incubation platforms described by Drew.

The platform, a 45 cms. square of well-varnished marine 5-ply board was laid on the sea-bed and anchored by karabiniers to two heavy weights (old cast-iron harpoon heads of 20lbs. each, used in whaling). The platform did not need to be raised above the sea-bed as P. grandifolius has a very short, flexible stipe relative to frond length, giving no support whatsoever to the frond which thus lies flat over the sea-bed. There was enough play in the tethering lines to permit some movement of the platform, but not enough to cause damage with increased turbulence. Four glass Kilner jars of 460mls. volume for incubation of algal discs

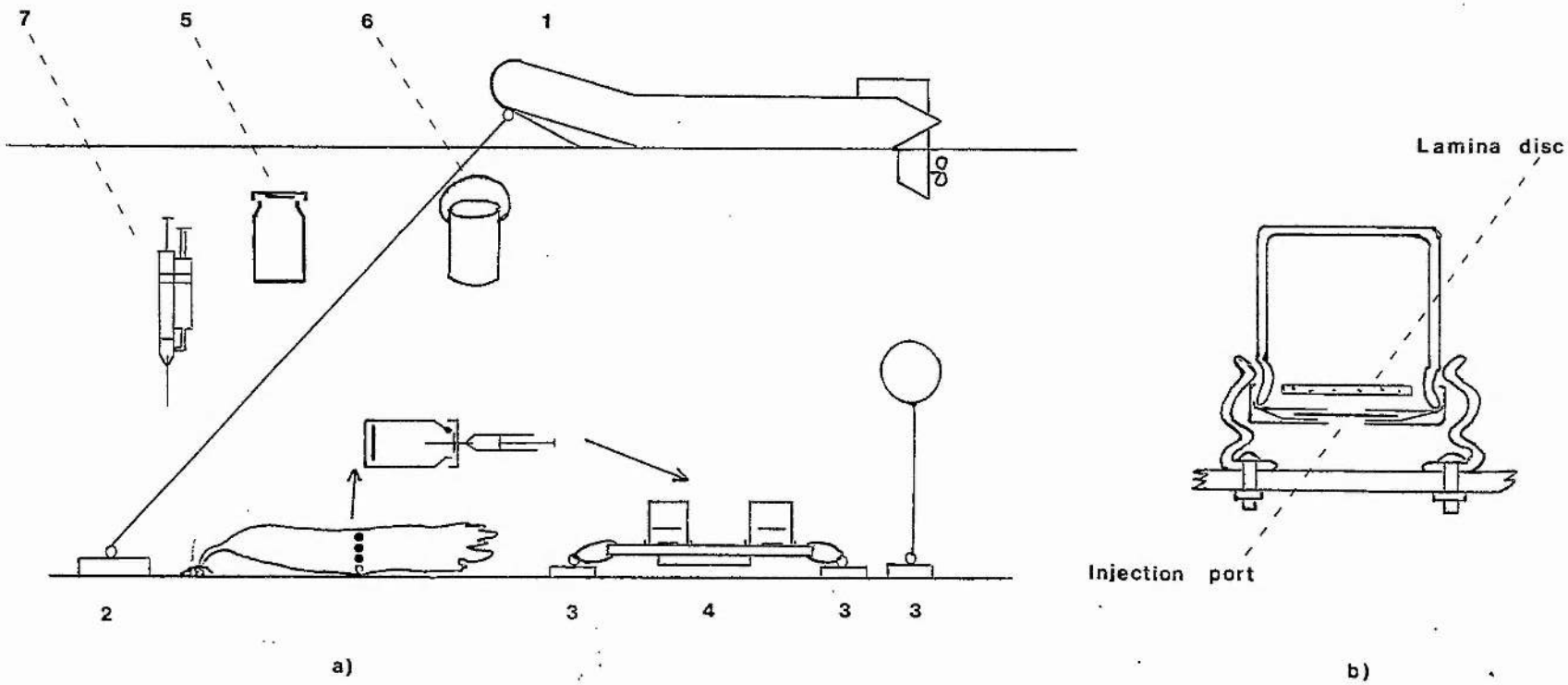

Fig. 3.1 (a) Schematic diagram of apparatus used in ^{14}C experiment
(b) Detail of attachment of Kilner jar to incubation platform
(numbers refer to summer equipment list in text)

were firmly held, bottom uppermost, by Terry clips on top of the platform. One of these jars was blacked out for dark incubation using tape and paint. The whole platform could be assembled in a few minutes and was strong enough to withstand considerable turbulence.

Equipment used

a. Summer

1. Boat, boatman, diving gear
2. Permanent mooring for boat
3. Marker buoy and anchors
4. Incubation platform
5. 4 Kilner jars with self-sealing rubber injection ports in lids
6. Tissue cutter
7. Repeating syringe
8. Black polythene bag
10. Large plastic bucket

b. Winter

1. Snowmobile, 12ft. Nansen sledge, driver/linesman
2. Diving gear plus safety lines
3. Chain saw and marker flag for hole
4. Protection for divers against wind chill after dive
5. Remaining equipment as in summer.

Method

A permanent summer mooring for the boat was laid about 12m.

from the sampling site and a marker buoy secured near the platform anchors. This buoy was on 1.5m of rope and thus always submerged to prevent ice-floes carrying it away. Both platform anchors and the marker buoy were left on site.

The platform was clipped to the anchors by diver 1 while diver 2 cut the necessary algal discs with the cutter (half a tin can, diameter 6.5m.). The discs for each experiment were cut close together at a point where it was possible to cut four discs traversing the lamina thus minimising any metabolic differences within the lamina. Discs for subsequent experiments were cut in similar fashion from adjacent parts of the lamina (see Fig. 3.2); once that lamina was 'used up' further discs were cut as described from a second lamina of the same plant. This was sufficient for all the experiments at that site. When the discs were in the jars and the tops screwed on, diver 1 injected each jar with a saline solution of C14 sodium bicarbonate of 10uCi.ml^{-1} using a repeating syringe. The syringe operated by drawing the isotope from the reservoir chamber through a non-return valve into the delivery barrel in volumes of about 1ml. This approximation was corrected for by subsequent determination of the specific radioactivity of the seawater from samples taken from each of the jars. After injection, the jars were shaken, clipped into position and the discs thus incubated horizontally. The incubation period was four hours from 10a.m. till 2 p.m., this being the period of maximum illumination and minimum variation in surface light intensity.

Recovery of the apparatus took no more than five minutes and was usually carried out by one diver. The four jars were placed in a large black polythene bag, effectively stopping photosynthesis. For ease of carrying the bag was placed in a plastic bucket and the platform was also

lifted. See Fig. 2.1

On return to the laboratory the jars were removed from the bag, in dim light. Water samples were taken from each jar and stored at $-40^{\circ}C$ in labelled 20ml Jorgensen tubes. The tissue was then washed in fresh seawater and immersed in 20mls 80% ethanol in a 28ml Jorgensen tube, shaken vigorously to kill the entire tissue disc and also stored in the dark at $-40^{\circ}C$.

All operations involving the use of C14 labelled compounds in the laboratory were carried out over a large metal tray, any waste material being stored for later disposal in accordance with the articles laid down in the Antarctic Treaty.

Analysis of tissue samples

Owing to the necessarily restricted facilities available in the Antarctic, laboratory analysis of the tissues was delayed until return to the U.K. By this time some of the tissues had been stored in 80% ethanol for over two years, without any visually apparent deterioration.

The alcohol extraction was completed using three further changes of boiling 80% ethanol; all four extracts were then combined and made up to a standard volume of 50mls. The dry weight of the alcohol insoluble tissue was determined after drying the tissue in an oven at $80^{\circ}C$ for twelve hours. This tissue was then fragmented into a boiling tube and 2mls. sulphuric acid added. Hydrolysis was carried out for three hours in a boiling water bath with foil caps over the tubes to prevent losses by evaporation. The hydrolysate was then decanted off, the residue washed three times with distilled water and all solutions combined to make a

standard volume of 15mls.

The residue remaining in the boiling tubes was allowed to soak in tap-water overnight to remove all traces of acid. The water was discarded and the residue dried. Radioactivity in each of the three fractions: alcohol, hydrolysate and insoluble residue were then determined as follows:-

a. Alcohol soluble

Aluminium planchets of 3 cms. diameter were warmed on a slide warming tray at 40°C and a ring drawn around the circumference with a wax pencil to prevent edge-creep of solutions. 0.1ml of the alcohol extract was pipetted onto the planchet together with a drop of acetic acid to release any inorganic C14 remaining. Two replicates of each sample were prepared and the planchets dried on the slide-warming tray.

b. Acid hydrolysate

1ml of the solution was neutralised with excess barium carbonate in a centrifuge tube, centrifuged in an MSE bench centrifuge for 5 minutes and the pH checked with Universal Indicator Paper 0.25ml aliquots were then dried on planchets, two replicates being prepared. Wax rings were not needed.

c. Insoluble residue

The acid insoluble residue was pulverised while wet, spread thinly over planchets and allowed to dry on a slide warming tray. Any curling of the tissue was flattened carefully as flat geometry was essential for the counting procedure. The weight and area of the residue on each planchet was determined after drying so that a correction for the self-absorption of radioactivity, within the samples could be applied. (see section on 'Corrections to observed counting rates').

Analysis of water samples

a. Storage of samples

20mls seawater from each incubation jar were stored at $-40^{\circ}C$ in a 25ml Jorgensen tube. They were then thawed immediately prior to analysis, the extra 5mls allowing room for expansion.

b. Inorganic carbon content

0.6ml $^{N}/_{20}$ sulphuric acid was added to 10mls seawater and the solution was boiled. This drove of all carbon dioxide from carbonate, bicarbonate and dissolved carbon dioxide and left some sulphuric acid unneutralised. The amount of acid left was determined by titration with $^{N}/_{500}$ sodium hydroxide using Universal Indicator. (Grey end-point, pH 4.6). An example of the subsequent calculations is set out below:

Say titration value of 1ml $^{N}/_{500}$ NaOH

$\equiv$ 0.04ml $^{N}/_{20}$ NaOH

$\therefore$ 0.56ml acid used up

or $\frac{0.56}{20}$ ml N acid used. $10ml^{-1}$

or $\frac{0.56 \times 100ml}{20}$ N acid used. 1^{-1}

$=$ 2.80ml N acid

$\equiv$ 0.00280 eq. 1^{-1} acid or CO_2

$\therefore$ $-\delta$ gives 0.00278 g.mols. $c.l^{-1}$ where $\delta = 0.00002$ eq.

1g. mol = 12g.C

$\therefore$ 0.00278 x $12g.l^{-1}$

or 0.00278 x $12mg.ml^{-1}$

or 278 x $12ug.ml^{-1}$

$=$ $33.36ug.C.ml^{-1}$

c. Radioactive content

The inorganic carbon in the seawater samples was precipitated

as barium carbonate by addition of 2mls. saturated barium chloride solution to 1ml seawater in a centrifuge tube. The resulting precipitate was washed twice with hot distilled water to remove traces of barium chloride and the washings were discarded. 1ml distilled water was used to resuspend the precipitate and two replicates of 0.25ml of this suspension were pipetted onto planchets and dried as previously described. Knowing the weight of the planchet, the weight of the precipitate could be found by difference. This was necessary as a correction for self-absorption of radioactivity within the precipitate had to be made.

Counting equipment for measurement of radioactivity

Planchets from all fractions, prepared as above were counted for three 10-minute periods each in a Nuclear Chicago gas-flow proportional counter with an automatic sample changing facility and a capacity of 50 planchets. The gas used was 90% argon plus 10% methane and the equipment was characterised by a short dead time (6usec), low background and an efficiency of about 20% for C14 when thin end windows were used.

Each group of 50 planchets included a standard - emitting source (a piece of radioactive perspex) to check the calibration of the counter, ensuring it was operating at the same level of efficiency for each set of samples. The level of background radiation varied over the range 9-13 counts per minute (cpm), however even the lowest levels of activity recorded for the samples were at least one order of magnitude higher and thus the results were seen to be clearly significant without using statistical tests.

Corrections to observed counting rates

The mean of the three readings obtained was converted to counts

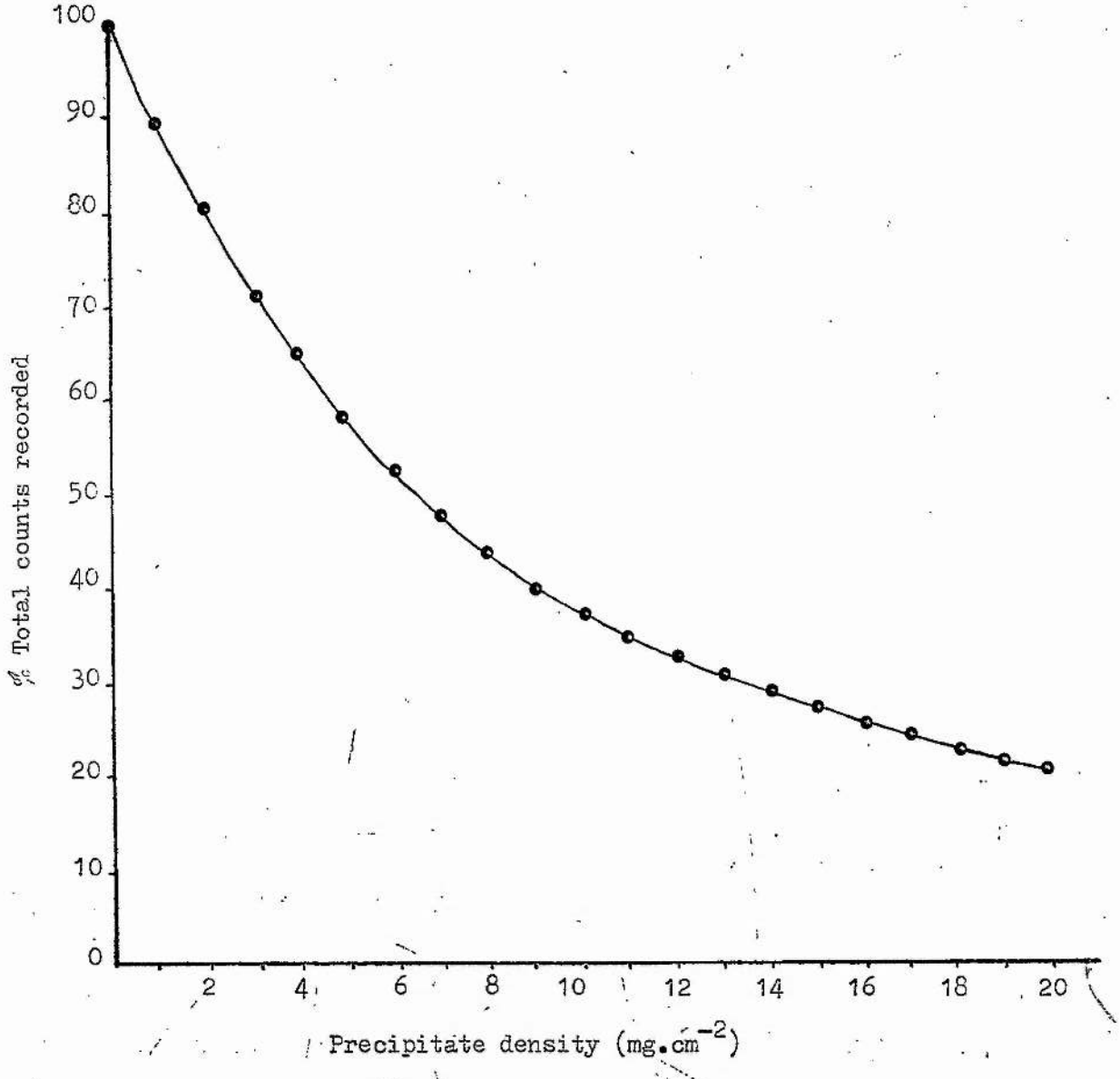

Fig. 3.2 ^{14}C Self-absorption curve for thin precipitates

represents net, gross or an intermediate value will be considered later.

Example of results from in situ ^{14}C experiments

Two specimen calculations are set out below representing a very low rate of $14CO_3^{--}$ fixation and a very high rate. That these very different rates were found the same month, but in consecutive years is explained in the Discussion.

Table 1. November 14th, 1973

	COUNTS			Total Counts	Specific Activity Seawater	T/SAS	UgC. $cm^{-2}.h^{-1}$	PHS L-D
	Alcohol	Hydrol.	Residue					
L1	6000	900	306	7206	14.90	483.62	3.66	3.07
L2	6000	720	417	7137	15.56	458.68	3.47	2.88
L3	6500	540	1019	8059	17.53	459.73	3.48	2.89
D	-	-	949	949	12.27	77.34	0.59	

Mean = 2.95

Table 2. November 7th, 1974

	COUNTS			Total Counts	Specific Activity Seawater	T/SAS	UgC. $cm^{-2}.h^{-1}$	PHS L-D
	Alcohol	Hydrol.	Residue					
L1	89500	7980	7973	105453	120.39	875.93	6.64	6.35
L2	69500	6000	6642	82142	89.99	912.79	6.92	6.63
L3	111000	9960	7331	128291	132.27	969.92	7.35	7.06
D	4500	300	211	5011	132.84	37.72	0.29	

Mean = 6.68

per minute and corrected for background radiation. A correction for dead time was not applied as the count rate was not high enough to warrant it.

Self absorption corrections were not needed for the low density ethanol extracts and acid hydrolysates but were applied to the denser barium carbonate precipitates and the tissue residues. The counts obtained were corrected to "infinite thinness" using a correction curve drawn from data in the Radiochemical Handbook (See Fig. 3.2).

Calculation of primary production

Planchets were counted using normal counting procedures and the carbon uptake determined from the formula:

$$\frac{a + i + r + y}{s} \qquad \text{UgC. cm}^{-2}\text{. h}^{-1}$$

where a = alcohol soluble counts per minute. cm^{-2}. h^{-1}
i = acid hydrolysate cpm. cm^{-2}. h^{-1}
r = insoluble residue cpm. cm^{-2}. h^{-1}
y = dark jar fixation cpm. cm^{-2}. h^{-1}
s = specific activity of experimental seawater in cpm. Ug^{-1} inorganic carbon

The columns labelled 'COUNTS' in Tables 3.1 and 3.2 show the figures obtained after applying the previous corrections. The total counts were converted to UgC using the specific radioactivity of each water sample. This value represented Ug carbon for the whole algal disc over the period of the experiment; therefore to convert to UgC. cm^{-2}.h^{-1} the value was divided by 132 (disc area, 33cm^2 x time, 4 hours). Finally the dark fixation was subtracted to give the photosynthetic rate. Whether this

IV WINKLER OXYGEN DETERMINATIONS

Respiration was studied using the Winkler technique to determine the response of Phyllogigas to varying external environmental conditions. With samples for the in situ photosynthesis experiments being taken from adjacent places along the lamina each week it was thought necessary to check how the respiration rate varied along the lamina with increasing distance from the meristematic region.

Tissue for use in Winkler analyses was stored in running seawater in dim light; never for more than 24 hours before it was needed. Segments of tissue were cut from the mid-line of the lamina, starting near the stipe where the width of the lamina was only 2cm. The narrowing of the lamina in this area produced the irregular area of the first segments (see Fig. 3.3), determined by tracing an outline onto graph paper and counting squares. Subsequent segments were all of $25cm^2$. After weighing the tissue segments were incubated in amber 'polystop' bottles of about 165mls volume. The bottles, usually nine in number, including one 'blank' without tissue, were carefully filled underwater in a bucket of fresh seawater to exclude all air bubbles and placed in a seawater bath held at $-1^{\circ}C$. This temperature could be accurately maintained by a refrigerated cooling coil and some small pieces of ice floating in the water. A propeller ensured adequate circulation of the water. The period of incubation was four hours after which the bath was emptied. No allowance was made for phytoplankton or bacterial respiration or their seasonal variation other than the 'blank' bottle.

Experimental analysis

The method outlined in Strickland & Parsons (1965) was followed

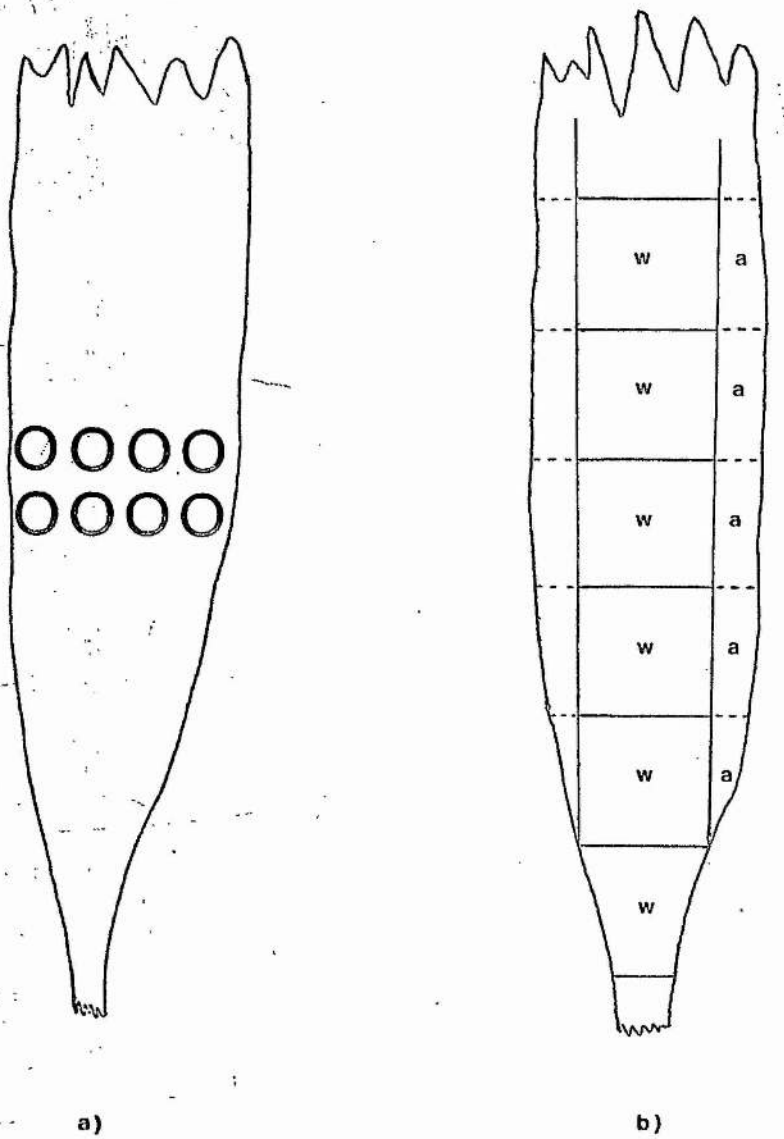

Fig. 3.3 Diagram to illustrate the position of tissue discs cut in various experiments.

a. In situ ^{14}C experiments, circular discs cut across the lamina; 4 per experiment.

b. Winkler oxygen determinations, square tissue segments (W) cut longitudinally from the midline of the lamina; the edges of the lamina (a) being used for ashing experiments.

throughout except that after dissolving the precipitate in the BOD bottle with concentrated sulphuric acid, the resulting solution was poured off the algal tissue and aliquots were then taken for analysis in the normal way. When the analysis was complete the bottles were thoroughly washed with seawater and distilled water to remove traces of chemicals before the next incubations.

Sample calculation

1ml 0.0089N thiosulphate $\equiv$ 50µl O_2

titre x 50 $\equiv$ µl O_2 per 50ml sample

$\frac{\text{titre} \times 50 \times \text{bottle vol.}}{50 \text{ (sample vol.)}}$ $\equiv$ µl O_2 per bottle

$[O_2]_{SW} - [O_2]_{RB}$ $\equiv$ O_2 used by $25cm^2$ in 4 hours

$\therefore [O_2]_{SW} - [O_2]_{RB}$ $\equiv$ µl $O_2 . cm^{-2} . h^{-1}$ consumed

$\therefore [O_2]_{SW} - [O_2]_{RB} \times 0.54$ $\equiv$ $\mu gC . cm^{-2} . h^{-1}$

assuming 1µl O_2 = 0.54µgC

Where results have been analysed statistically, standard significance tests as outlined in Bailey (1966) were used.

V CARBOHYDRATE ANALYSIS BY GAS-LIQUID CHROMATOGRAPHY

The alcohol extracts prepared in the analysis of the *in situ* ^{14}C experiments were used to determine the seasonal variation in the content of mannitol. It was studied as it is an important storage carbohydrate in *Phyllogigas*, a primary product of photosynthesis, and an important respiratory substrate.

A Pye Unicam Automatic Preparative Chromatograph (Series 105, Model 15) was used in a single column analytical form and gave rapid estimations of mannitol within five minutes of sample injection. (See

Holligan & Drew, 1971, for details of this system). The apparatus consisted of a 5' x $\frac{1}{4}$" (1.524m x 0.635cm) internal diameter glass column with a glass/metal outlet to a flame ionisation detector. This detector was used in conjunction with a Leeds and Northrop 'Speedomax' pen recorder with a disc integrator.

Column packing and support material

The support phase was acid washed siliconised Diatomite C (60–72 mesh) and the liquid stationary phase was 1% SE 52 silicone gum. These were prepared as described by Holligan & Drew. The column was packed by application of a moderate vacuum at the outlet.

Preparation of volatile derivatives

2.5mls of the alcohol extract (in a 35ml Jorgensen tube) were dried in a vacuum desiccator over calcium chloride; atmospheric moisture being removed later by a rotary evaporator run at 60°C. The volatile trimethylsilyl (TMS) derivative of mannitol was prepared by redissolving the dried ethanol extracts in 0.85ml pyridine and adding 0.1ml hexanmethyldisilazane (HMDS) and 0.05ml trimethylchlorosilane (TMCS) giving a reaction volume of 1.0ml. After vigorous shaking the reaction mixture was allowed to stand overnight at room temperature before analysis, allowing time for the reaction to proceed to completion. (Tight-fitting plastic lids kept out any moisture.) (Over 90% of the reaction can be expected in five minutes at room temperature with these reagents).

Injection of samples

10ul aliquots of the silylated derivatives were injected rapidly onto the column which was run isothermally at 175°C. Due to lingering impurities in the samples it was found that consistently accurate

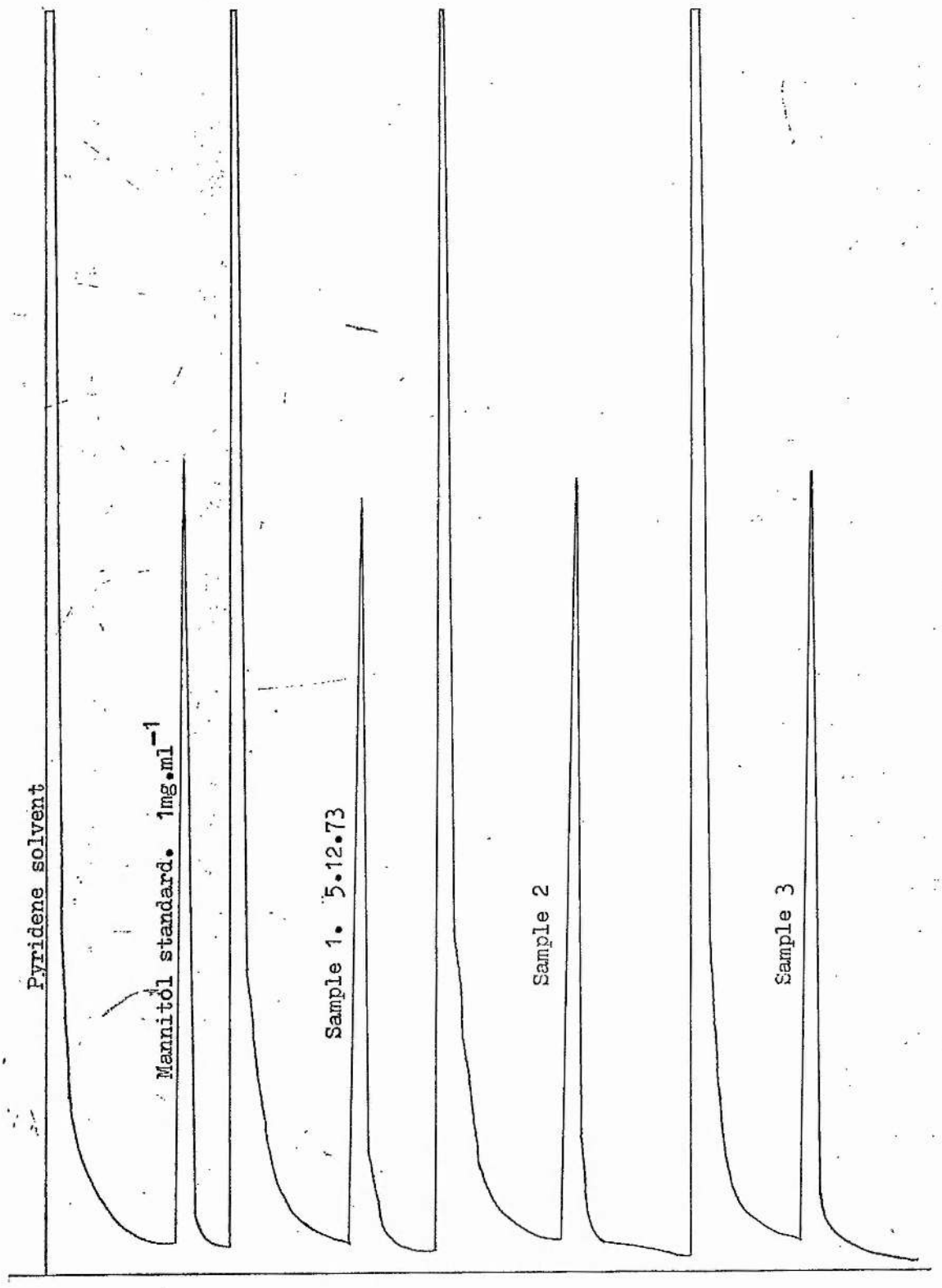

Fig. 3.4 Typical GLC traces of mannitol, using a 5' glass column packed with 2% SE 52 on diatomite 'C'. Temperature programme isothermal at 175°C attenuation 2 x 10^4

results could only be achieved by raising the column temperature to 300°C for five minutes after each "run". The carrier gas was oxygen-free nitrogen at a column pressure of 5 psi and a rate of flow of 60ml min^{-1}. hydrogen at 20 psi and 30 ml. min^{-1} and air at 60 psi and 500ml. min^{-1} were supplied to the flame ionisation detector. Two replicates of each sample were run and every fifth run a standard was injected.

Identification and quantitative estimation of peaks

A single peak was produced on the chromatograms from all samples during these analyses. The retention time, from the time of injection to the vertical edge of the solvent peak was measured and similar retention times to an authentic standard of mannitol was considered as evidence of chemical identity. Typical GLC traces are shown in Fig. 3.4.

The peak areas were determined from the response of a disc integrator attached to the recorder; values were corrected for base-line deflection. The linear response of the flame ionisation detector and disc integrator for calibration curves with TMCS derivatives of standard sugars shown by Holligan & Drew indicate the reliability of this technique.

To determine the peak area of each sample, the base-line correction was subtracted from the integrated area. The base line correction is the product of base line deflection (% fsd), base line peak width and integrator response at 1% full scale deflection.

Example of calculations

Sample	Integrated Area	Base Line Deflection %	Base Line Peak Width %	Base Line Correction	Peak Area	Mg Mannitol
Standard	1060	7.0	7.0	270	790	1
L1	685	10.5	5.0	289	396	0.5
	730	9.5	5.5	287	443	0.5
L2	360	1.0	6.5	36	324	0.6
	570	5.0	6.5	179	391	0.7
Standard	620	1.5	7.0	58	562	1
L3	280	4.0	4.5	99	181	0.3
	310	2.5	6.0	83	227	0.4
D	320	1.0	6.0	33	287	0.5
	365	1.5	6.0	50	315	0.6
Standard	565	1.0	7.0	39	526	1

Table 3.3. Sample results for 21.8.74 showing the stages in the calculation of the mannitol content of the tissue

Sample calculation

To determine the content of mannitol in each sample replicate the peak area of the standards must first be determined (Table 3.3).

(Concentration of standards: 1mg mannitol ml^{-1})

For the first standard, the base line correction is given by:-

	Base line deflection	x	B.L. Peak width	x	Integrator response	
=	7.0	x	7.0	x	5.5	
			= 270			
	Integrated area		= 1060			
	∴ Peak area		= 1060 - 270			
			= 790			
			≡ 1mg mannitol			

The peak areas of the sample replicates were similarly determined. By reference to the appropriate standard (i.e. the closest one on the chromatograph to that particular 'run') the mannitol level for that replicate was found.

This figure was then corrected for dilution of the extract, and the final figure, % mannitol in the extract determined by dividing by extract dry weight.

e.g. Sample L1 (see Table 3.5)

$$\frac{\text{Sample} \times \text{Dilution}}{\text{Extract Dry wt.}} \times 100 = \frac{0.5 \times 20}{340.4} \times 100$$

= 2.9% mannitol in sample extract

DATE: 27.2.74

Sample	Mg Mannitol	Mannitol (Mg) in Extract. Dil^{n}. x 20	Extract Dry Weight (Mg)	% Mannitol in Extract
L1	2.4	48	312.2	15.4
	2.5	50		16.0
L2	1.8	36	300.6	12.0
	2.0	40		13.3
L3	1.9	38	305.4	12.4
	1.9	38		12.4
D	2.2	44	307.2	14.3
	2.2	44		14.3

Mean = 13.8%

Tables 3.4 (above) and 3.5 (below) chosen to show the differences between summer and winter levels of mannitol in the fronds of Phyllogigas.

DATE: 21.8.74

Sample	Mg Mannitol	Mannitol (Mg) in Extract. Dil^{n}. x 20	Extract Dry Weight (Mg)	% Mannitol in Extract
L1	0.5	10	340.4	2.9
	0.5	10		2.9
L2	0.6	12	357.2	3.4
	0.7	14		3.9
L3	0.3	6	362.8	1.7
	0.4	8		2.2
D	0.5	10	405.7	2.5
	0.6	12		2.9

Mean = 2.8%

VI AN IN SITU GROWTH EXPERIMENT AT THE SHALLOW SITE/6.2m)

The reasons for setting up this experiment were as follows:

1. To determine the length of the growing season of Phyllogigas
2. To see how these results compared with the growing season as indicated by the in situ ^{14}C experiments
3. To ascertain, at least qualitatively, the effect of external environmental factors e.g., habitat, sea-ice, etc. on growth rate.

The plants were marked by a series of holes punched along the mid-line of the lamina, at least 2cm apart and starting from a point where the lamina was 2cm wide, so that its attachment to the stipe would not be weakened.

Measurements, using a 15cm plastic ruler were made weekly during the summer growth season and fortnightly during the winter months. The positions of the plants were marked by brightly painted corks on short lengths of string initially, but these were later removed once the positions had been learnt. This was because the lines became entangled with the stipes and caused some damage. The diameter of the holes was recorded in pencil on a 'formica' board, together with the total length of the marked strip.

Suitable laminae were selected with regard to their habitats, including sheltered and exposed cliff faces, gullies and gently-sloping rock/shingle sea-bed. Two laminae on one plant were measured to determine any significant differences in growth.

It was found that seven plants was the optimum number that could be monitored on one dive. More than this and cold had an increasingly

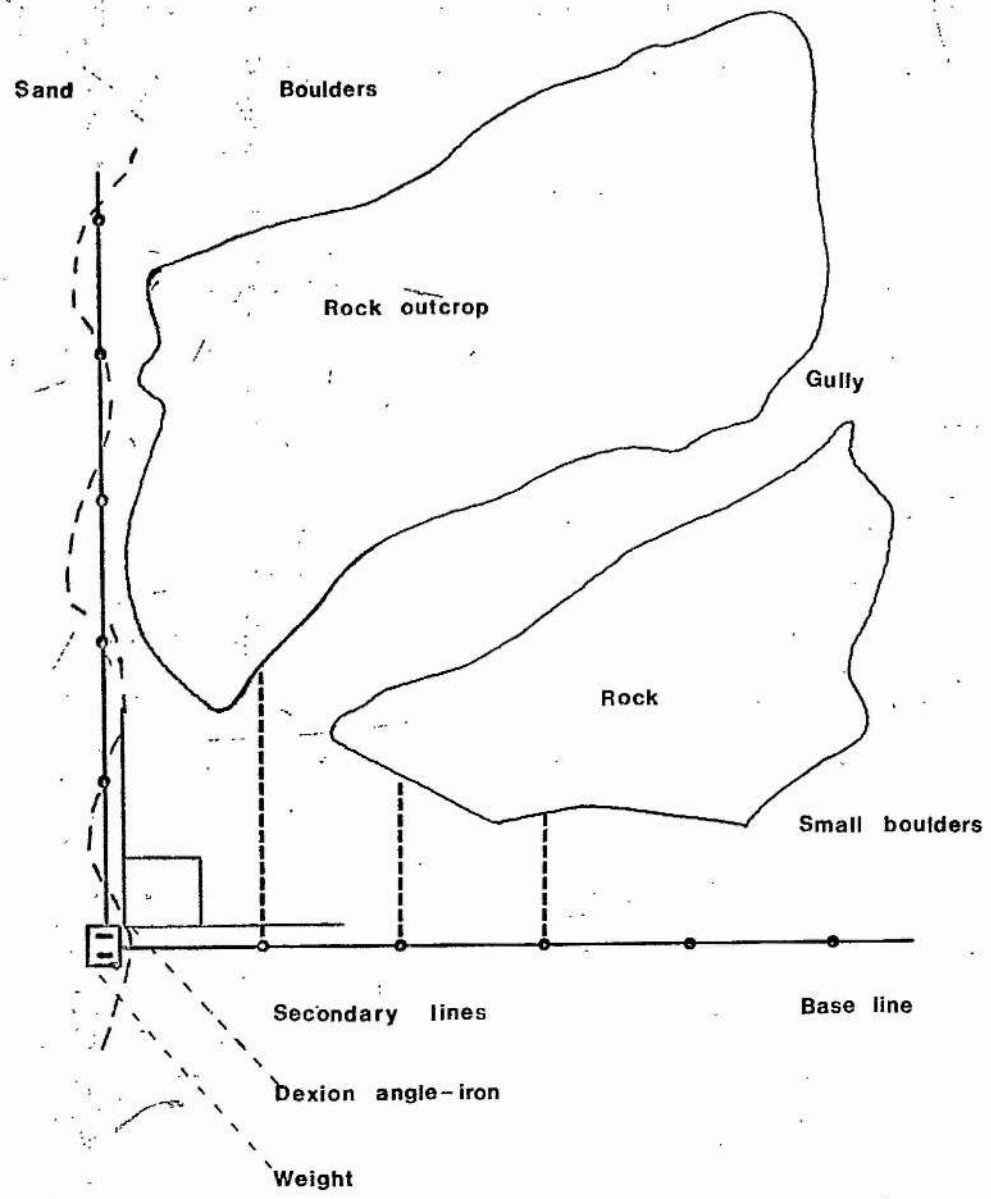

Fig. 3.4 Position of lines used in the mapping of the shallow site

detrimental effect on diver performance. Sampling was limited by the lack of abundance of plants and frequency of diving by logistic factors.

VII DISTRIBUTION OF ALGAE IN SHALLOW WATER

A detailed survey of the shallow site and its immediate vicinity was carried out for a number of reasons:

1. To determine the abundance and distribution of the flora in relation to the topography and substrate
2. To see if any zonation of the major algal groups existed
3. To gain an idea (with subsequent lamina area measurements of the biomass of Phyllogigas in that area
4. To gain some experience of underwater mapping techniques.

Mapping was carried out over the period 24.10.74 to 29.11.74, taking full advantage of the excellent visibility found with the presence of sea-ice. The break-out of the ice while still some 20cm thick on 30.10.74 interrupted the work and some points were rechecked in early January when the phytoplankton bloom was on the decline. The final area surveyed was 25m x 40m.

Initially a 40m base line was laid along the sand/rock boundary on the cove floor at approximately 7m (24') depth. This line, thin, orange polypropylene cord was knotted every 2m and marked with a piece of white tape every 10m, and its ends anchored with 4lb lead weights. At each end, lines were laid at right-angles running up to the cliff face and marked as before every 2 and 10m (see Fig. 3.4).

The corner angle was determined using a right-angle made of two 9ft lengths of dexion angle iron, bolted together on the bottom. With the excellent visibility there were no problems in lining up the ropes correctly. Three secondary lines were laid parallel to the base line and these, marked as before, formed 2m squares which were individually mapped. Divers engaged in mapping carried a set of formica boards marked out with a 4cm square grid. Different coloured 'Chinagraph' pencils were used to indicate rocks, algae, etc. (The final scale of the map was 2cm = 1m). As an area was completed the lines were leapfrogged up the slope and the process repeated until the cliff was reached. Other measurements, such as gully width were determined with a 2m pole.

After each dive the work was transferred from the mapping boards to a master copy on the same scale. Individual plants of Phyllogigas and Ascoseira were noted down and the Desmarestiales drawn in en masse with oblique lines. The red algae, mainly Plocamium, covered all boulders below 2m and for the sake of clarity were excluded from the final copy. A note on their distribution was included in the Key.

Within the area covered by the map, the surface areas of laminae of Phyllogigas were measured by two divers. One diver held a 1cm wide tape measure at the base of the lamina, where it was the same width as the measure and the second diver laid the lamina out flat and measured to the extreme tip. The maximum width was also noted. All the laminae measured showed signs of abrasion distally and along their lateral margins.

This method of measurement does not allow for any curvature of the lamina; it is assumed to be flat and regular whereas both lateral and horizontal curving are present. Corrections for this were applied by re-measuring in the laboratory several laminae previously measured underwater

and comparing the results. Two methods were used:

1. The outlines of some of the smaller laminae were traced onto graph paper and the squares counted.
2. A known area of lamina was weighed and compared with the total lamina fresh weight. Replicates were taken to allow for the decrease in lamina weight per unit area away from the meristem at the base of the frond.

These two methods agreed to within 6%; the field method gave results 30% larger than these.

VIII GROWTH RATE FROM NEW PLANTS

Four 'new' plants were found at the shallow site on 29.1.75 which were not recorded on the map. Their position, on a cliff face, meant they would have been torn off by the ice had they been there during the winter months. From this it was assumed that they were that season's growth, over a period of almost exactly three months.

Two plants possessed four laminae (A and B in the results) one had three (plant C) and plant D, two. The lengths and maximum widths of these 13 laminae were accurately measured and a note made of the habitat of the plants and the depth of water they were growing in. This for later comparison with the plants monitored in the in situ growth experiment.

IX BIOMASS PER UNIT AREA

Six plants were cleared from an area 93cm x 93cm at a depth of 9.2m (30ft) on a low cliff face near the deep site at Cam Rock. This site was chosen as having one of the denser, more even covers of Phyllogigas

of all the localities visited (see large-scale map of algal distribution).

The areas of the laminae, cut at the base of the stipe were found by placing a sheet of polythene marked with a 5cm grid over each lamina and counting the squares covered. Pressing the lamina flat to measure the area produced overlap of tissue around the 'pleats' in the lamina. This overlapping tissue was cut out of two laminae and its percentage of the total area estimated. This figure was then added to each lamina area.

X ASH CONTENT OF LAMINAE

All surplus water was removed from pieces of tissue of known area (generally 5 x 5cm, but if of irregular shape, an outline was traced onto graph paper). They were then weighed on a Mettler H15 balance and the tissue cut into quarters so that it would fit more easily into the ashing crucibles later. The samples were dried on clean glass petri dishes at 80°C for 24 hours. The brittle tissue was then weighed, ashed at 500°C for 24 hours in a 'Carbolite' electric furnace, and then reweighed.

XI BOMB CALORIMETRY

Pieces of lamina tissue which had been kept frozen at -20° to -40°C since collection were dried in an oven at 80°C for 24 hours. They were then weighed, broken into fine pieces and placed in nickel crucibles. The crucible was placed in the barrel of a Gallenkamp CB-370 Ballistic Bomb Calorimeter and the sample ignited at 25 atmospheres pressure of oxygen. The maximum deflection of the galvanometer connected to a thermocouple in the 'bomb' barrel was noted. This deflection was converted to kcal.g^{-1} by comparison with the deflections caused by the thermochemical grade benzoic

acid (6.32 kcal.g^{-1}). Assuming the temperature remained below 550°C at which temperature $CACO_3$ may be decomposed (Robertson, (pers. comm.) found this did not happen) the residue left in the crucible after ignition represents the ash contents of the tissue. This weight was subtracted from the initial dry weight to give the ash-free organic dry weight of the material.

XII MONITORING OF ENVIRONMENTAL FACTORS

Surface irradiance

The monthly irradiance figures plotted in Fig. 2 were obtained from a computer print-out of part of a long-term programme of terrestrial microclimate monitoring. Grant type D 20-channel recorders were used in conjunction with a Kipp and Zonen CM5 solarimeter.

Seawater parameters - light, temperature and chemistry

These measurements were carried out by Hoogesteeger and Tappin (BAS Scientific Reports) using the methods laid out in Strickland & Parsons (1965) with some modifications as a result of the climate. Sampling was done weekly, weather permitting, from a drifting boat during summer months, and through a hole cut in the ice during winter. Two sites were employed, one close inshore in Factory Cove, the other further offshore in Normanna Strait (see Maps 2 and 3).

The parameters measured included:

1. Light with depth using selenium photocell probe
2. Temperature and oxygen using a combined probe and reversing thermometers.

3. Salinity using low precision titration with $AgNO_3$.

4. Phosphate by the colorimetric method using the molybdenum blue reaction with phosphate.

5. Nitrate and nitrate levels using the colorimetric methods.

6. Ammonia by the Solorzano colorimeter method.

7. Chlorophyll 'a' and carotenoids using cold acetone extraction.

8. Silicon by silico-molybdate complex.

CHAPTER 4

RESULTS I. PHYSIOLOGICAL EXPERIMENTS: PHOTOSYNTHESIS AND RESPIRATION ANALYSES

I THE IN SITU ^{14}C EXPERIMENTS

Two sample sets of results are laid out in section Chapter 3, 'Materials and Methods'. They, together with the relevant calculations show how the figure for Gross Primary Production (expressed in $ugC.cm^{-2}.h^{-1}$) was arrived at in each case. The experiments were carried out over a period of 20 months, more frequently in summer than in winter. Some results had to be discarded due to their unreliability, most likely caused by the injection of unequal amounts of isotope due to the formation of ice in the syringe. This produced an irregular sampling interval, particularly at Cam Rock, the deeper of the two sites with a more exposed situation where conditions both in summer and winter did not always permit a dive.

The graphs illustrated are as follows:

Fig. 4.1 The shallow site curves:

a. Gross photosynthesis expressed as $ugC.cm^{-2}.h^{-1}$

b. Net photosynthesis (gross-respiration rate) expressed as $ugC.cm^{-2}.h^{-1}$.

c. Daily accretion in $ugC.cm^{-2}.d^{-1}$ taking into account the respiration rate (discussed more fully in Section II of this chapter) over 24 hours and the time available for photosynthesis, i.e. day-length. It is described by the equation below.

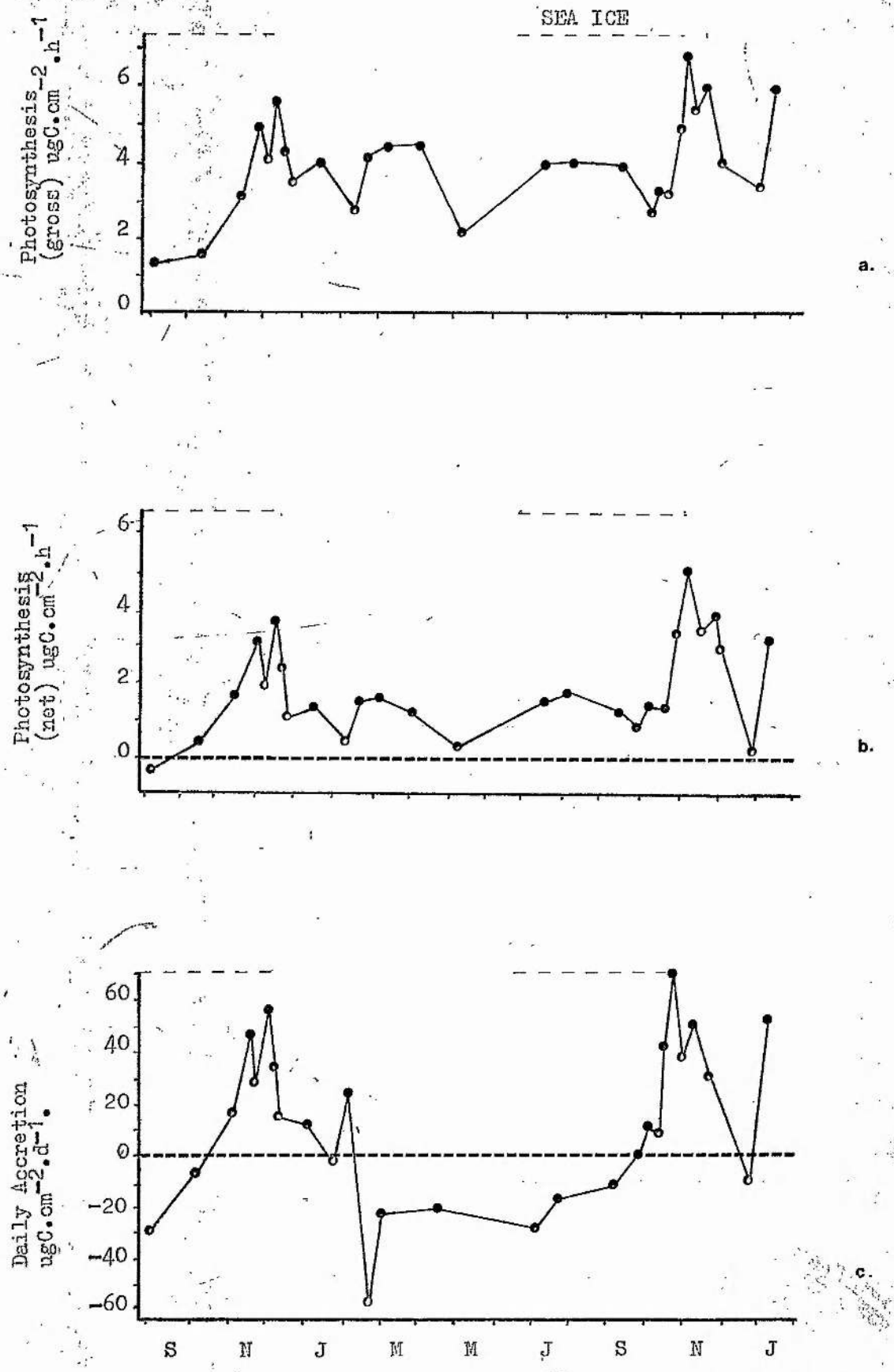

Fig. 4.1 The shallow site ^{14}C curves over a period of 14 months. a and b. Gross and net photosynthesis in ugC.cm^{-2}.h^{-1}. c. Daily Accretion in ugC.cm^{-2}.d^{-1}.

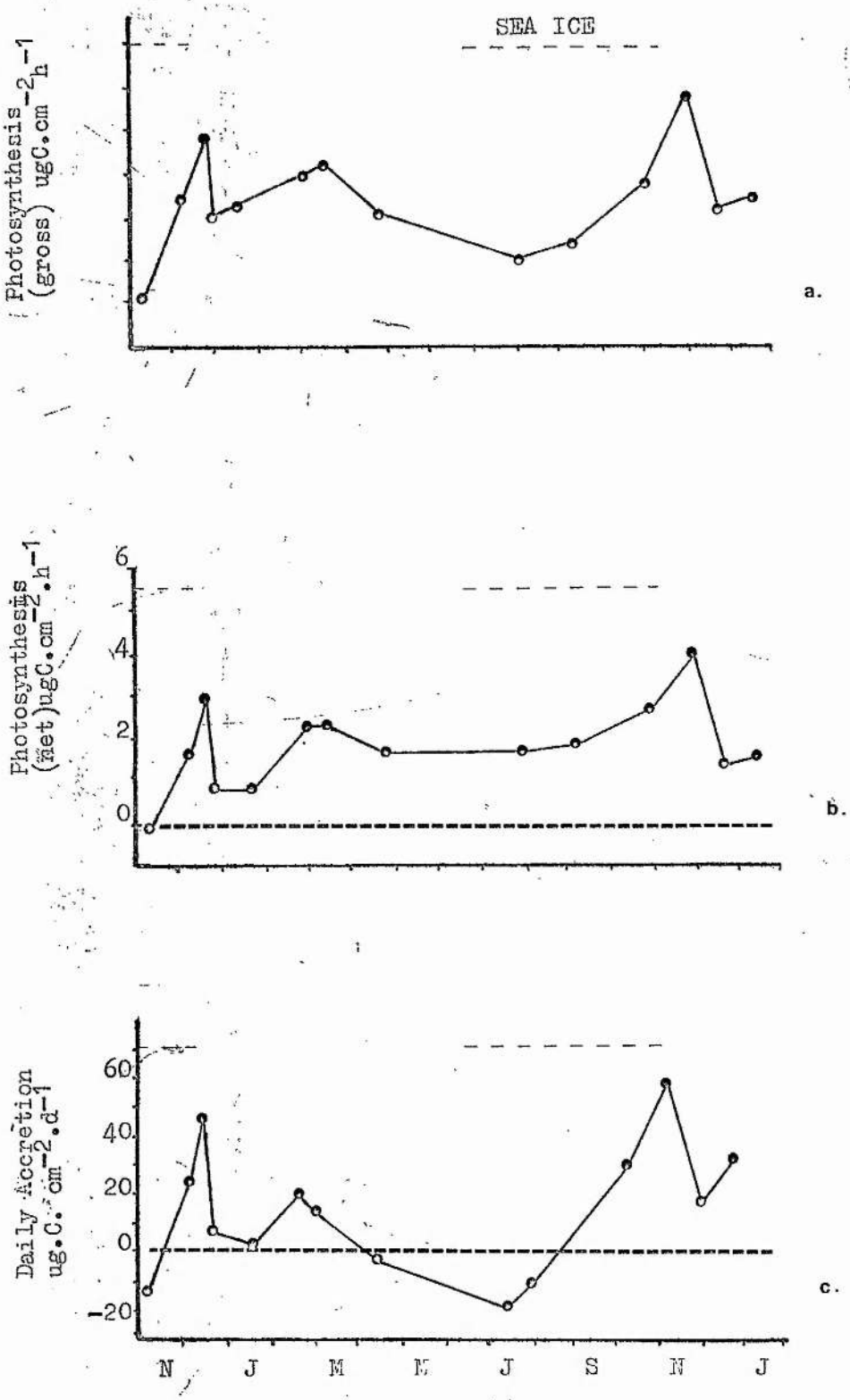

Fig. 4.2 The deep site ^{14}C curves over the some period as Fig. 4.1. Graphs a, b and c as in Fig. 4.1 for comparison with duration of sea ice shown at top of each graph.

Fig. 4.2 The deep site curves, a, b and c as in Fig. 4.1 for ease of comparison.

The data for these curves are tabulated in Tables 4.1 and 4.2 respectively. For the sake of accuracy and clarity the standard errors of the results were not drawn in but are included in the tables. Units as for graphs.

Shallow Site

Date	Results (Gross PHS)	Mean with STD Error	Mean Net PHS	Daily Accretion
5. 9.73	1.13	1.25	- 0.45	- 27.61
	0.56	± 0.44		
	2.07			
15.10.73	1.61	1.45	0.30	- 7.04
	1.53	± 0.12		
	1.22			
14.11.73	3.07	2.95	1.55	14.81
	2.88	± 0.06		
	2.89			
28.11.73	4.87	4.79	3.12	46.25
	5.85	± 0.66		
	3.64			
5.12.73	3.72	3.86	2.05	29.37
	3.95	± 0.07		
	3.90			
12.12.73	6.81	5.37	3.64	55.12
	4.18	± 0.77		
	5.11			
19.12.73	5.32	4.23	2.33.	33.97
	3.16	± 0.62		
	4.21			
26.12.73	2.93	3.38	1.21	14.03
	4.20	± 0.41		
	3.01			
21. 1.74	3.01	3.84	1.35	10.08
	3.91	± 0.46		
	4.61			

(contd.)

Shallow Site

Date	Results (Gross PHS)	Mean with STD Error	Mean Net PHS	Daily Accretion
13. 2.74	2.64	2.63	0.38	- 4.24
	3.53	± 0.52		
	1.73			
27. 2.74	4.86	4.04	1.55	22.73
	4.08	± 0.49		
	3.17			
6. 3.74	3.08	4.36	1.62	- 58.66
	6.49	± 1.07		
	3.50			
3. 4.74	3.71	4.37	1.41	- 23.11
	2.92	± 1.08		
	6.48			
17. 5.74	2.97	2.16	0.57	- 20.05
	1.83	± 0.41		
	1.69			
18. 7.74	2.92	3.83	1.74	- 27.69
	1.83	± 1.49		
	6.74			
7. 8.74	2.62	3.89	1.93	- 15.92
	-	± 1.28		
	5.17			
19. 9.74	5.49	3.95	1.41	- 9.43
	3.46	± 0.79		
	2.89			
3.10.74	3.08	2.66	1.06	- 2.25
	2.80	± 0.29		
	2.09			

(contd.)

Date	Results (Gross PHS)	Mean with STD Error	Mean Net PHS	Daily Accretion
16.10.74	2.63	3.12	1.58	7.98
	3.07	± 0.30		
	3.66			
23.10.74	3.37	3.17	1.56	7.03
	3.06	± 0.10		
	3.09			
30.10.74	3.23	4.84	3.45	42.33
	8.29	± 1.73		
	3.00			
7.11.74	6.35	6.68	5.16	70.19
	6.63	± 0.21		
	7.06			
13.11.74	4.95	5.35	3.33	35.56
	6.55	± 0.61		
	4.54			
20.11.74	5.47	5.85	3.65	49.67
	6.86	± 0.51		
	5.22			
29.11.74	5.28	3.91	3.11	27.91
	5.08	± 1.27		
	1.37			
1. 1.75	3.66	3.26	0.57	9.78
	2.79	± 0.25		
	3.33			
8. 1.75	7.60	5.99	3.44	53.87
	–	± 1.61		
	4.38			

Table 4.1 Summary of <u>in situ</u> photosynthesis data for the shallow site in Factory Cove for a period of 16 months. Standard errors of mean gross photosynthesis data are included.

Deep site

Date	Results (Gross PHS)	Mean with STD Error	Mean Net PHS	Daily Accretion
2.11.73	1.08	1.25	- 0.19	- 14.43
	1.19	± 0.12		
	1.48			
5.12.73	3.22	3.45	1.69	21.59
	3.85	± 0.20		
	3.28			
19.12.73	5.89	4.90	2.94	46.55
	4.22	± 0.51		
	4.58			
26.12.73	2.59	3.05	0.87	6.24
	3.07	± 0.25		
	3.46			
21. 1.74	4.21	3.30	0.92	2.94
	2.73	± 0.46		
	2.98			
29. 2.74	4.18	4.07	2.42	19.01
	3.73	± 0.18		
	4.31			
6. 3.74	5.48	4.36	2.43	13.52
	3.04	± 0.71		
	4.59			
16. 4.74	3.68	3.16	1.71	- 3.83
	3.81	± 0.58		
	2.01			
22. 7.74	1.48	2.09	1.66	-19.85
	2.99	± 0.46		
	1.81			

(contd.)

Deep Site

Date	Results (Gross PHS)	Mean with STD Error	Mean Net PHS	Daily Accretion
28. 8.74	2.71 3.46 1.43	2.53 ± 0.59	1.88	- 10.05
26.10.74	5.12 2.88 3.79	3.92 ± 0.65	2.72	28.82
22.11.74	6.36 5.58 6.21	6.05 ± 0.24	4.00	56.68
14.12.74	2.89 4.23 3.52	3.55 ± 0.39	1.45	16.76
4. 1.75	3.56 4.05 3.67	3.76 ± 0.15	1.60	31.91

Table 4.2 Summary of in situ photosynthesis data for deep site at Cam Rock, including standard error of mean gross photosynthesis observations, over a period of 14 months. Negative values of daily accretion occur only during winter months.

D.A. = GROSS PHOTOSYNTHESIS x DAY LENGTH − RESPIRATION x 24
($ugC.cm^{-2}.h^{-1}$) ($ugC.cm^{-2}.h^{-1}$)

Table 4.3. below shows the final results used in the calculation of daily accretion for the deep site.

Gross P.	Respiration	Net P.	Day Length	G.P.xD.L.	R.x24	D.A.
2.09	1.39	1.66	6.6	13.79	33.36	-19.85
6.05	2.05	4.00	17.5	105.88	49.20	56.68

Table 4.3. Maximum and minimum values of daily accretion (D.A.) calculated according to the equation above. Examples taken from the deep site at Cam Rock; minimum 22.7.74 and maximum 22.11.74

Shown on each graph is the duration of the sea ice during the winter months. The effect of the ice on irradiance levels in the water is discussed in Chapter 2; for further details; thickness of ice, nature of upper surface etc., see Appendix 3.

The similarity of shape between the curves for net and gross photosynthesis (best seen in the curves for the shallow site), shows how little the respiration rate changes during the year. The curves for the shallow site are considered first.

A positive daily accretion figure is first observed in late October 1973 and again, at the same time of year, early October 1974. In both cases, it will be noted, the sea ice was still present so nothing near the total irradiance available was reaching the algae (See Fig. 2.6b). The daily accretion then increased rapidly to a maximum value which in both

summers occurred soon after the departure of the sea ice. These maxima were observed in early December 1973 and almost a month earlier in 1974, in early November. The close correlation between these dates and the departure of the sea ice is immediately apparent. The daily accretion is then seen to decrease almost as rapidly as it increased, finally falling below the Compensation Point in late February 1974. Data for the end of the second summer were not obtained.

The extremely low result recorded in March 1974 might be considered as an example of the effect of increased turbidity on daily accretion. At the end of February 1974, a prolonged, severe storm threw much of the bottom sediments into suspension. These had not entirely settled out by the time the March observation was made, with consequent lowering of light levels. By the time of the next experiment the sediments had completely settled out and the rate had risen once again. Although the rate rose it did not regain its previous level above the Compensation Point and remained 'negative' for the next $7\frac{1}{2}$ months of winter.

The curves for the exposed site at Cam Rock, while not so detailed for reasons already explained do nonetheless show the main trends of the daily accretion. Again the curve can be divided easily into three parts: two summer maxima and a winter minimum.

A positive daily accretion figure is first observed in mid November 1973 and in early September 1974. More frequent sampling in 1974 would probably have shown this to occur in early October instead. Again, the sea ice was still present when positive accretions were first observed, which then increased rapidly reaching a maximum about a week later than at the shallow site, after the sea ice had blown out. (Mid December 1973 and mid November 1974 at Cam Rock, as opposed to early December 1973 and early

November 1974). These increases were again followed by almost equally rapid decreases.

A secondary maximum was observed towards the end of February 1974 at both sites though slightly later again at Cam Rock. Both curves also show an increase in the rate of daily accretion at the end of December 1974; that of the shallow site being far more marked, going from negative to positive. The possible reasons for these features will be considered in the Discussion.

The effects of the late February storm in 1974 are not known at Cam Rock as sea conditions took longer to stabilise there than at the sheltered shallow site. It would however seem reasonable to assume on the basis of the observed results at the shallow site that a similar occurrence took place at Cam Rock thus pushing the daily accretion level below the Compensation Point earlier than shown, increasing again the period of negative winter values.

At Cam Rock the overall levels of accretion were seen to be lower than at the shallow site as would be expected but there remains an obvious similarity in shape of the two daily accretion curves.

Photosynthetic efficiency

The results from the bomb calorimetry work produced a figure for the mean calorific content of lamina tissue of 3.9 kcal. per gram organic matter. If it is assumed the carbon content of organic matter is 47% (Westlake, 1963), it is possible to calculate the calorific content of carbon: 8.3 $kcal.gC^{-1}$.

or 0.0083 $cal.ugC^{-1}$

Site	Date	Gross PHS	Total Surf. Rad.	Visible Radiation* available	Effect-ive Day Length (total-2h)	P.E.%
Shallow	5. 9.73	1.25	156.7	0.688	10	14.5
	12.12.73	5.37	343.2	75.50	18	1.1
Deep	5.11.73	1.15	336.1	7.66	16	1.9
	14.12.73	4.91	425.8	59.61	18	1.2

Gross photosynthesis in $ugC.cm^{-2}.h^{-1}$

Surface radiation in $cal.\ cm^{-2}.d^{-1}$

*The radiation available (to the plants) is that fraction of the surface radiation in the visible part of the spectrum, 40% and corrected for attenuation in water (and ice during winter) reaching the plants, in $cal.cm^{-2}.d^{-1}$.

Table 4.4 Stages in the calculation of photosynthetic efficiency (P.E.) assuming irradiance utilized over a period of day length less 2 hours, allowing for sunset.

The radiation available to the plant has to be corrected for day-length, discounting an hour either side of sunset. This figure is then the radiation available in $cal.cm^{-2}.d^{-1}$. The gross photosynthesis can then be expressed in $cal.ugC^{-1}$ by multiplying by 0.0083 $cal.ugC^{-1}$. The efficiency can then be found.

The samples chosen represent the maximum and minimum values of gross photosynthesis at each site.

Summary of Results

From these results, four main points can be brought out. These will be considered in greater detail in the Discussion in Chapter 6.

1. A positive daily accretion occurs only during the summer months.
2. The plants at the deep site have a lower daily accretion than those at the shallow site.
3. The duration of the growing season is influenced by the presence of sea ice and day length.
4. Phyllogigas is shown to have a low photosynthetic capacity.

II RESPIRATION EXPERIMENTS

In most of the respiration experiments samples of tissue were taken along the length of the frond to see if there was any marked variation in respiration with position. Some typical results are set out in Table 4.5 below:

Stipe	Area (cm^2)	Respiration Rate $ugC.cm^{-2}.h^{-1}$	Respiration Rate $ugC.g^{-1}Divt.h^{-1}$	Fresh Weight (g)	Ash Weight / Fresh Weight %
↑	16	1.41	6.18	1.3389	-
	19	1.56	5.98	1.5318	-
	25	1.98	6.09	1.9072	11.11
	25	1.43	4.17	2.0124	10.74
	25	1.75	5.49	1.8679	9.14
	25	1.72	5.81	1.7379	7.64
	25	1.61	5.65	1.6713	6.55
Lamina Tip ↓	25	1.57	6.63	1.3906	4.87

Table 4.5. Typical results from a Winkler experiment (30.9.74) showing position, area, fresh weight and ash weight as % fresh weight of lamina segments used. The respiration rate is expressed on an area ($ugC.cm^{-2}.h^{-1}$) and dry weight ($ugC.g^{-1}$dry wt.h^{-1}) basis and shows how this rate varies from the narrowing base of the lamina (hence the smaller area) to the lamina tip.
(See Fig. 3.3)

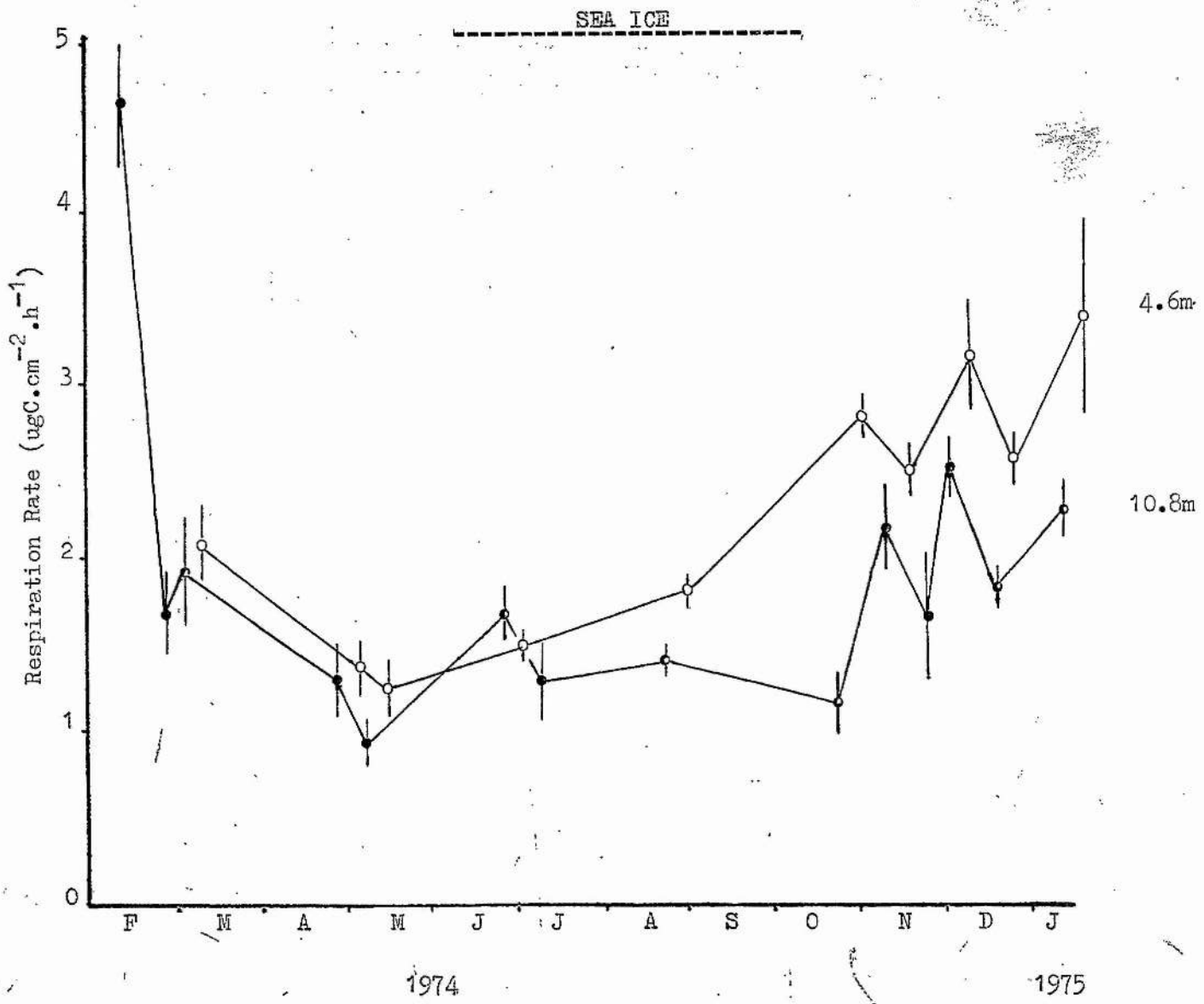

Fig. 4.4 Variation in Respiration rate at different depths at the deep site over 1 year. Standard errors and duration of sea ice shown.

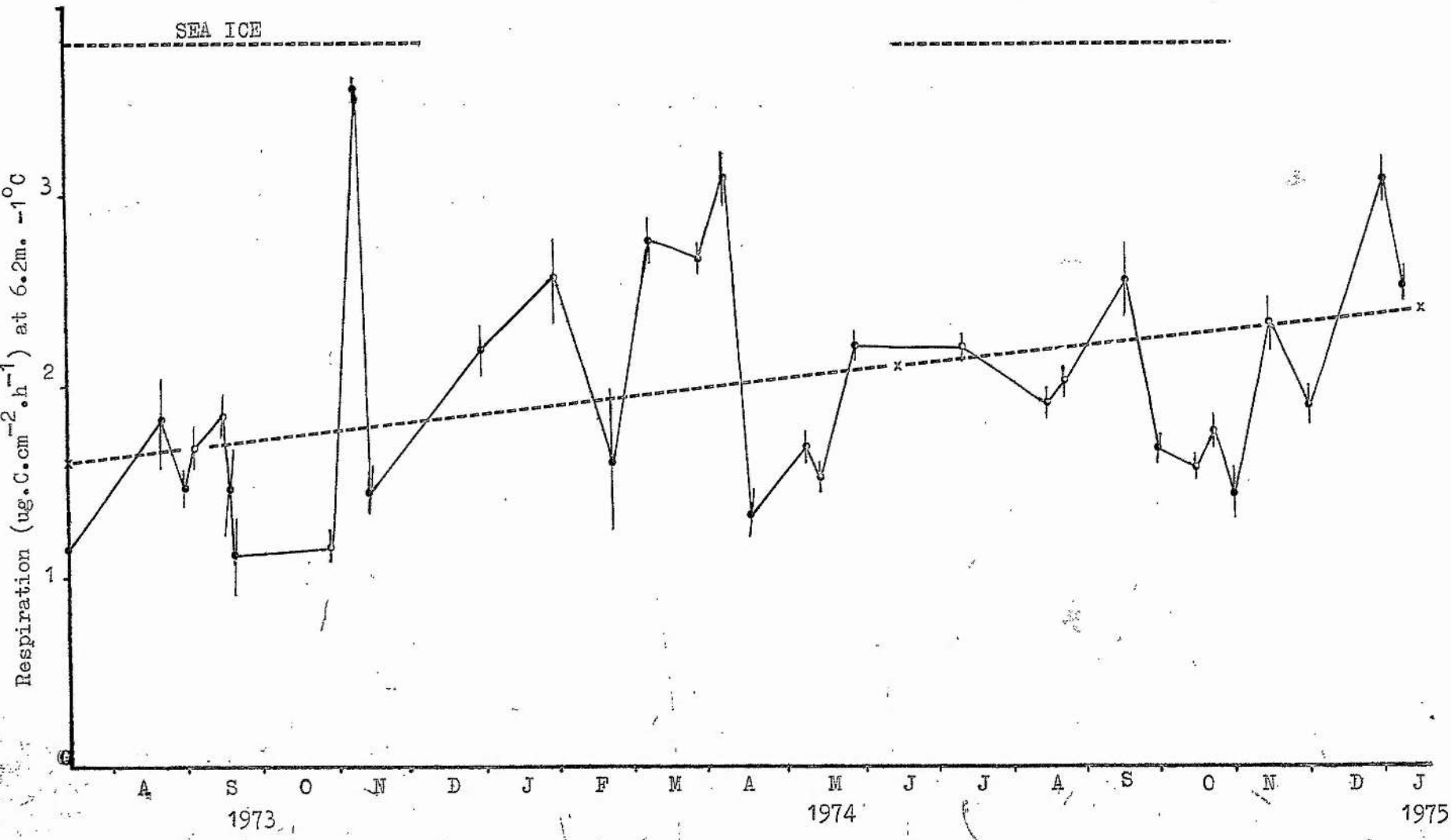

Fig. 4.3 Seasonal variation of respiration of Phyllogigas grandifolius at 6.2m. and -1°C. over a period of 19 months with fitted regression line and standard errors. Duration sea ice shown at top of graph.

The mean of such a series of results was then plotted to produce the respiration curves shown in Figs. 4.3 and 4.4. The figures show that there is a maximum value a little above the base of the lamina (about 10cm). More will be said about this in the Discussion, Chapter 6.

Figs. 4.3 and 4.4 show the seasonal variation in respiration at the two study sites. Fig. 4.3 is for the shallow site (6.2m) over a period of 19 months from July 1973 to January 1975, and Fig. 4.4 shows a two-depth analysis over a period of 12 months from February 1974 to January 1975 at Cam Rock the deeper site further offshore.

A regression line, described by the expression:

$$y = 1.58 + 0.04x$$

has been fitted to the shallow site curve using standard regression analysis techniques. Significance tests as laid out in Bailey (1966) were also carried out to determine whether any difference existed between winter and summer rates of respiration.

Respiration appears unaffected by the presence of sea ice as the following experiment shows.

The effect of open water and consequent increase in irradiance on respiration during winter

Introduction

Often during the winter months, movement of the pack ice, under the influence of wind, currents or tides, produced leads or areas of open water. These leads remained 'open' for periods as long as 10 days before freezing over again. One such lead occurred off Bernsten Point (see Map.3.) from 5th to 12th August 1974.

Results

The two tables below show the results obtained from two samples, both taken on the same day. One was growing directly under the lead in 6m water, free from overshadowing by the edge of the ice and the second from the same depth under approximately 0.75m ice at the shallow site. The respiration rate per gram dry weight was found by converting the fresh weight of tissue used in the experiments to its equivalent dry weight by multiplying by Dry Weight/Fresh Weight %. The respiration rate in $ugC.cm^{-2}.h^{-1}$ was then divided by this figure to give the rate per gram dry weight of tissue.

Biomass					Winkler	
Fresh Wt.	Dry Wt.	Ash Wt.	Tissue Fresh Wt.	Area (cm^2)	Respn. Rate $ugC.cm^{-2}.h^{-1}$	R.R.g^{-1} D.Wt.
1.5590	0.5346	0.1433	2.2025	18.5	2.60	4.11
1.4659	0.6929	0.1351	2.3703	22.0	2.52	3.61
1.2861	0.5126	0.1033	2.5432	21.5	2.41	3.22
0.9407	0.4199	0.0748	2.1649	18.0	2.12	3.33
0.3094	0.1803	0.0398	2.3270	25.0	1.47	2.15
2.1475	0.2556	0.0755	2.2085	25.0	1.45	2.23
1.2304	0.3933	0.1142	2.3363	25.0	1.52	2.21
1.5752	0.4088	0.1188	2.4716	25.0	1.85	2.54
2.0593	0.3021	0.0886				

Table 4.6 Results obtained from sample at Bernsten Point in 6m water after 7 days without ice cover. Biomass samples taken from alongside Winkler segments. (See Fig. 3.3) calculation of respiration rate per gram dry weight explained in text. Date 12.8.74

Biomass					Winkler	
Fresh Wt.	Dry Wt.	Ash Wt.	Tissue Fresh Wt.	Area (cm^2)	Respn. Rate $ugC.cm^{-2}.h^{-1}$	R.R.g^{-1} D.Wt.
1.4026	0.3197	0.0728	3.4164	24.5	2.25	3.58
2.0041	0.4041	0.0876	4.1420	28.0	2.14	2.81
2.9704	0.5675	0.1353	3.3298	25.0	2.26	3.69
3.3534	0.5941	0.1511	3.1146	25.0	1.81	3.16
3.0673	0.5188	0.1363	3.0893	25.0	1.56	2.75
2.6140	0.4836	0.1206	3.2076	25.0	1.63	2.76
3.0036	0.5051	0.1387	3.0149	25.0	1.61	2.90
2.6922	0.4888	0.1340	2.6148	25.0	1.58	3.29

Table 4.7 Results obtained from Shallow Site sample in 6m without open water. Date 12.8.74

Parameter	Bernsten	Shallow Site
Fresh Wt.	1.3971 ± 0.19	2.6385 ± 0.23
Dry Wt.	0.4110 ± 0.05	0.4852 ± 0.03
Ash Wt.	0.0993 ± 0.01	0.1221 ± 0.03
Loss Organic Wt.	1.2978	2.5164
$^{AW}/_{DW}$ %	24.16	25.16
$^{DW}/_{FW}$ %	29.42	18.39
R.R. g^{-1} D.Wt.	2.93 ± 0.26	3.12 ± 0.13

Table 4.8 Means with standard errors of parameters in Tables 4.6 and 4.7. Bernsten sample after 7 days open water and hence maximum irradiance levels, shallow site sample with approx. 0.5m ice cover.

The third table of results above shows the means of the data in Tables 4.6 and 4.7. A significance test was carried out on the respiration rates and it was found that there was no significant difference ($p \gg 0.1$).

All the results in Table 4.8 show a close similarity except the fresh weight figures. This is probably due to the greater area of tissue used in four of the eight Shallow Site samples compared with those from Bernsten. This in turn accounts for the variation in Dry Weight/Fresh Weight % figures.

From these figures it is clear that changes in the level of irradiance during the winter months has little effect, if any, on the respiration rate or tissue composition Phyllogigas.

The two curves from the Cam Rock site were also analysed to determine any significant differences:

a) between depths

b) between seasons for each curve

In the case of Cam Rock, there was no significant difference between the two depths ($p > 0.1$). However, as the following experiment shows, respiration rate can change with depth.

A Comparison of the respiration rate and tissue composition of samples from differing depths

Method

The plants observed at 32.3m (105ft) were massive in appearance compared with those at shallower depths. For example fronds with widths in excess of 50cms (1.75ft) were seen, though the plants themselves were few in number and widely scattered. Samples were collected from this depth and from 10.8m and 6.2m (35ft and 20ft) and the results shown in Tables 4.9, 4.10 and 4.11.

Results

The respiration rate per gram dry weight was calculated as previously. Table 4.12 summarises the data obtained.

Biomass					Winkler	
Fresh Wt.	Dry Wt.	Ash Wt.	Tissue Fresh Wt.	Area (cm^2)	Resp^n.Rate $ugC.cm^{-2}.h^{-1}$	R.R.g^{-1}D.Wt.
1.0035	0.2083	0.0525	1.9330	17	1.95	16.71
0.6881	0.1754	0.0382	2.9160	25	2.24	12.72
1.7623	0.3617	0.0858	3.0011	25	2.19	12.09
1.1323	0.1384	0.0369	2.8943	25	2.19	12.53
1.2898	0.2337	0.0586	2.9151	25	2.23	12.67
1.8479	0.1609	0.0341	2.8270	25	2.29	13.42
0.7066	0.1142	0.0449	2.8411	25	2.28	13.29
0.6071	0.1044	0.0371	2.6062	25	1.98	12.58

Table 4.9 Results obtained for 32.3m sample Biomass samples taken from alongside Winkler segments (See Fig. 3.3) Respiration rate per gram dry weight calculated as previous. Date 22.11.74 after 23 days open water.

Biomass					Winkler	
Fresh Wt.	Dry Wt.	Ash Wt.	Tissue Fresh Wt.	Area (cm^2)	Resp^n.Rate $ugC.cm^{-2}.h^{-1}$	R.R.g^{-1}D.Wt.
0.3636	0.0956	0.0062	0.9876	23	2.04	8.83
0.8294	0.1773	0.0242	1.0443	22	2.11	8.64
0.4931	0.0988	0.0467	1.0109	25	1.81	7.66
0.5820	0.1192	0.0189	0.8421	25	1.43	7.26
0.5971	0.1451	0.0563	0.8134	25	1.66	8.72
0.2730	0.0814	0.0320	0.7475	25	1.64	9.38
0.4151	0.1029	0.0299				

Table 4.10 Results for 10.8m sample. Caption as in Table 4.9.

Biomass					Winkler	
Fresh Wt.	Dry Wt.	Ash Wt.	Tissue Fresh Wt.	Area (cm^2)	Respn.Rate $ugC.cm^{-2}.h^{-1}$	$R.R.g^{-1}.D.Wt.$
0.8690	0.1859	0.0443	2.0411	24	2.64	9.41
1.1195	0.2506	0.0563	1.5704	25	2.68	12.41
1.0800	0.2159	0.0512	1.7397	25	2.54	10.62
1.6514	0.3576	0.0811	1.5291	25	2.09	9.94
1.2289	0.2429	0.0646	1.5235	25	2.10	10.02
1.5424	0.3068	0.0768	1.7512	25	2.18	9.05
1.3536	0.2860	0.0737	1.5218	25	1.85	8.84
1.0968	0.2362	0.0569	1.6632	25	2.23	9.75

Table 4.11 Results for 6.2m sample Biomass samples taken from alongside Winkler segments (See Fig. 3.3) Respiration rate per gram dry weight calculated as previous. Date 22.11.74 after 23 days open water.

Parameter	32.3m	10.8m	6.2m
Fresh Weight	1.1297 $\pm$ 0.17	0.5187 $\pm$ 0.07	1.2427 $\pm$ 0.09
Dry Weight	0.1871 $\pm$ 0.03	0.1213 $\pm$ 0.01	0.2602 $\pm$ 0.02
Ash Weight	0.0439 $\pm$ 0.01	0.0288 $\pm$ 0.01	0.0631 $\pm$ 0.01
Loss Organic Wt.	0.1432	0.0925	0.1971
AW/DW %	23.46	23.74	24.25
DW/FW %	16.56	20.35	13.75
$R.R.g^{-1}$ Dry Wt.	13.25 $\pm$ 0.52	8.42 $\pm$ 0.32	10.01 $\pm$ 0.40

Table 4.12 Means of parameters considered in previous three tables, with standard errors. Date 22.11.74, after 23 days of open water.

Tests were carried out to determine whether there was a significant difference between respiration rates at 32.3m and 10.8m and between 32.3m and 6.2m. In both cases the results were highly significant ($p < 0.001$). The biomass results showed little variation, even allowing for the differences in morphology of the plants and the more stable environment of the 32m plant.

The curves at Cam Rock also showed a significant difference between seasons, with the 10.7m curve showing the greatest ($p < 0.01$). This result might be due to the extremely high figure recorded for February. The shallower curve only showed significant differences at the 10% level.

Comparing all three curves for the period February 1974 to January 1975 it appears that conditions at the shallow site, as might be expected from its sheltered situation, are more stable. The respiration rate varies from 1.28 to 3.05 $ugC.cm^{-2}.h^{-1}$ (both occurring in April) whereas at Cam Rock, the maximum (4.7 $ugC.cm^{-2}.h^{-1}$) occurs in February and the minimum (0.95 $ugC.cm^{-2}.h^{-1}$) in May, a range of over twice that of the shallow site. The mean respiratory rates are given below for this period:

SITE	CAM ROCK	CAM ROCK	SHALLOW SITE
UNITS	10.7m	4.6m	6m
$ugC.cm^{-2}.h^{-1}$	1.91	2.18	2.14
$ugC.g^{-1}dwt.h^{-1}$	3.89	3.03	4.86

and there is little variation between them on an area basis but a significant difference between the shallow site at 6m at the Cam Rock site of 4.6m ($p < 0.01$). The difference between the 6m and 10.7m sites was only significant at the 10% level.

Summary of Results

The main points shown by these results and listed below will be treated further in the Discussion.

1. The respiration rate is low throughout the year.
2. The results at the shallow site vary over the range 1.15 to 3.56 $ugC.cm^{-2}.h^{-1}$, a difference of over 300%, but even at its highest, the result is still low.
3. Regression analysis showed a gradual increase in respiration rate at the shallow site over the period of observation.
4. Respiration was maximal at the base of the lamina and lower along the remainder.
5. Some seasonal variation was shown to exist at the deep site but not at the shallow site, where the rates were very similar ($p \cdot 0.1$).
6. Subsidiary experiments showed respiration to be unaffected by the presence or absence of sea ice, and to increase with depth.

CHAPTER 5

RESULTS II: NON PHYSIOLOGICAL EXPERIMENTS

INTRODUCTION

This chapter considers the results obtained from experiments measuring various parameters concerned with growth rates, overall biomass of Phyllogigas, "tissue composition" and the seasonal variation of these factors.

The parameters considered are:

I In situ growth

II Lamina areas, growth rates of four young plants at the shallow site and the biomass per unit area.

III "Tissue composition", including mannitol, expressed as % dry weight, calorific values of the lamina tissue, dry weight and ash-free dry weight of lamina tissue.

I IN SITU GROWTH

Graphs are presented (Figs. 5.1 - 5.7) of the rates of elongation of seven laminae in differing habitats at the shallow site, measured over a period of 8-16 months. Six plants in all were monitored; two laminae (Figs. 5.2 and 5.3) were on the same plant to see if there was any appreciable difference between their growth rates. The rate of elongation of the 10 punched holes, variations in this rate along the laminae, changes in lamina width and changes in the overall length of the strip of tissue containing the holes are considered. The distance between the holes was

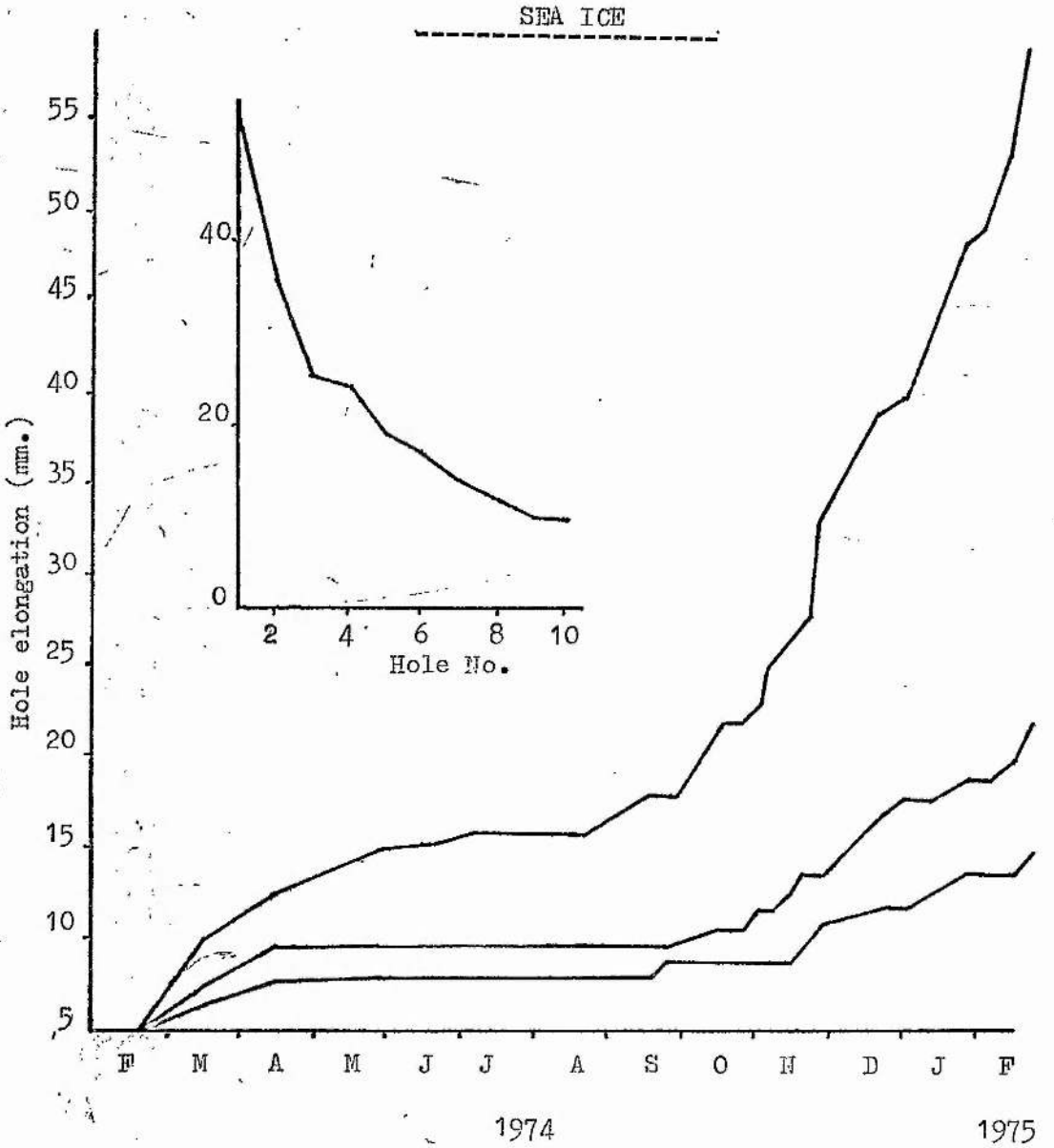

Fig. 5.1 Linear growth as indicated by hole elongation (mm) over 13 months. Inset shows maximum elongation of individual holes over period of observation. Duration of sea ice at top of graph.

Plant 1

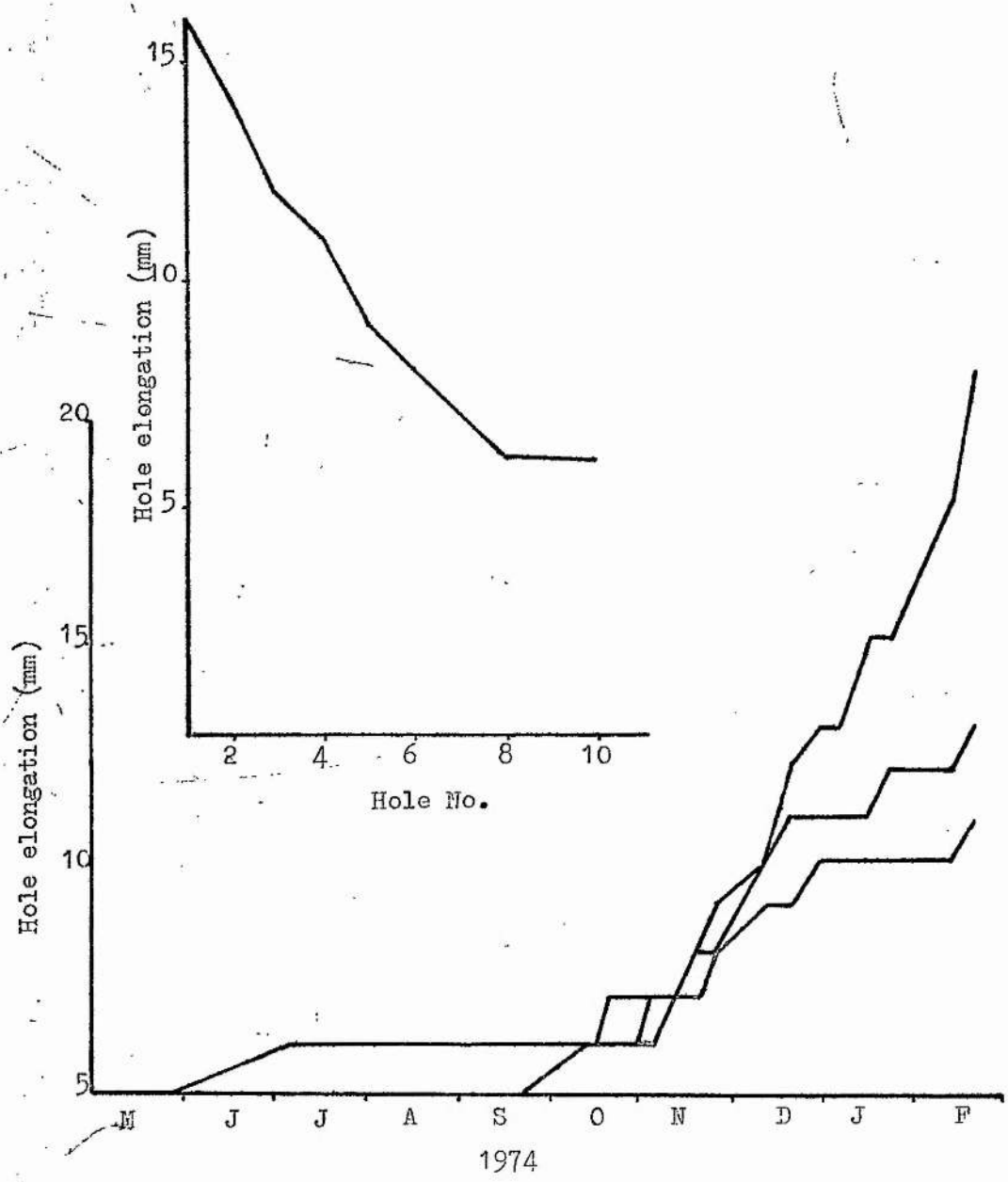

Fig. 5.2 Linear growth as indicated by hole elongation (mm) over 10 months. Inset as Fig. 5.1

Plant 2a

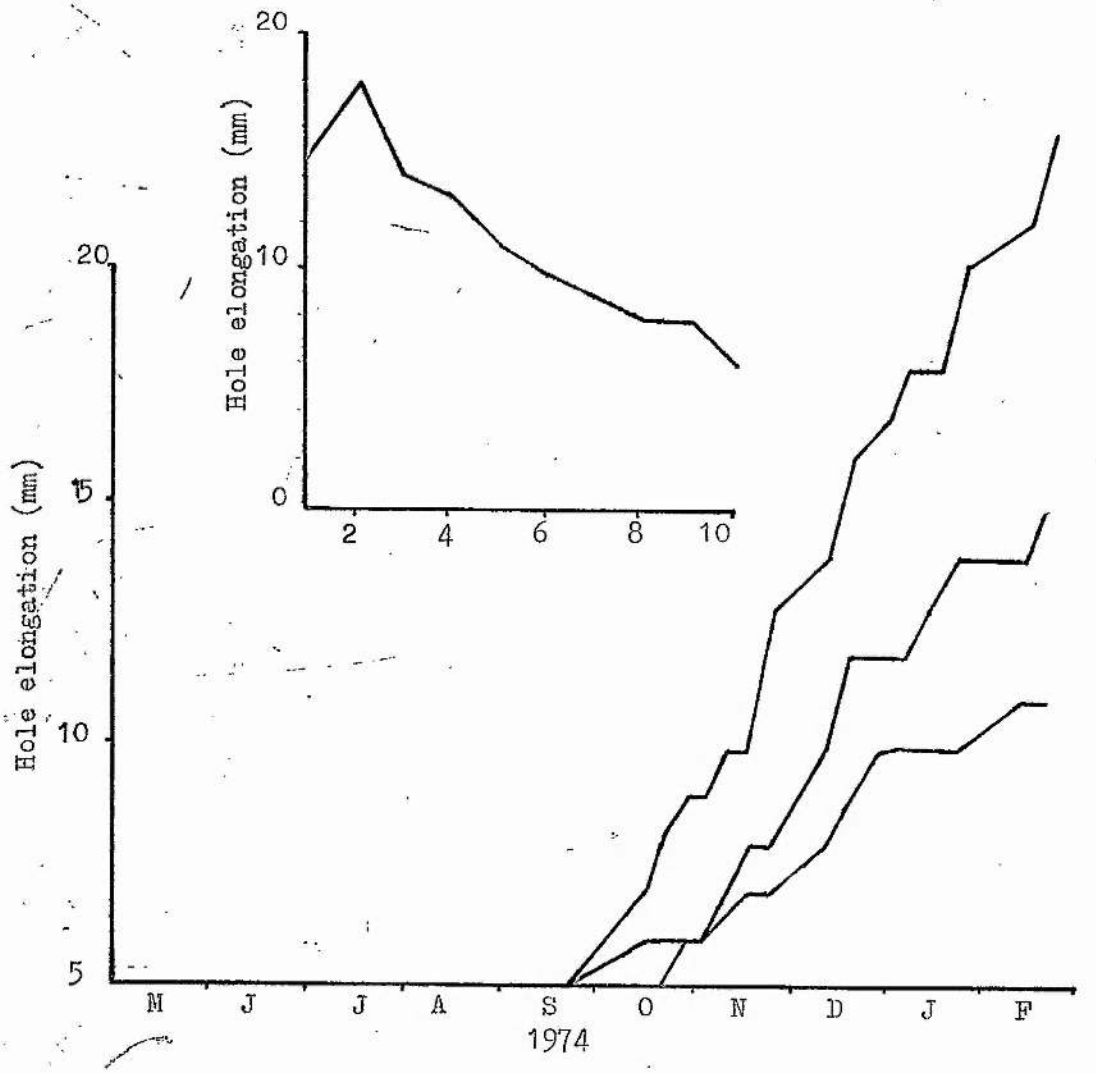

Fig. 5.3 Linear growth as indicated by hole elongation (mm)

Inset as Fig. 5.1

Plant 2b

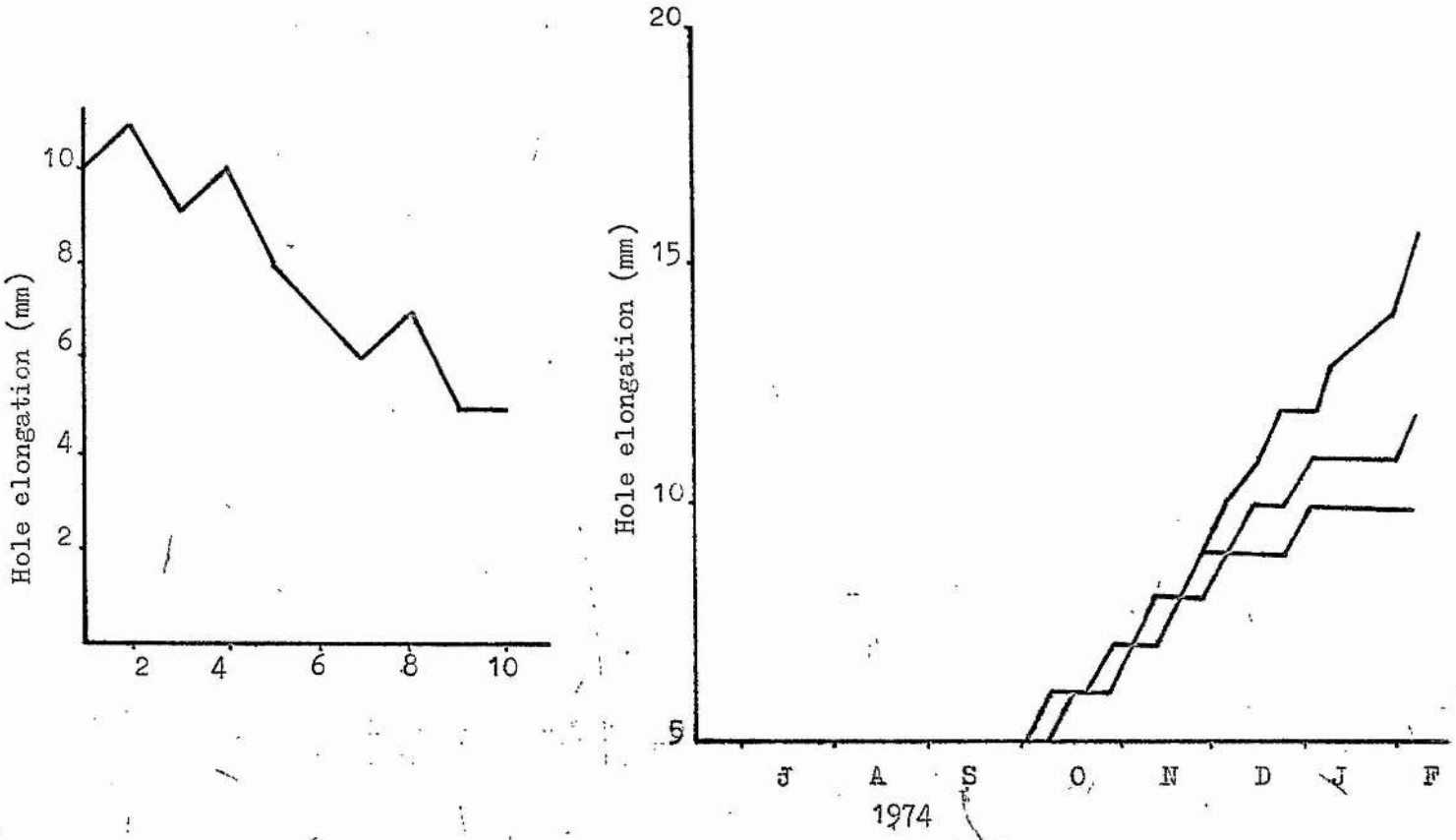

Fig. 5.4 Maximum elongation of individual holes (mm) over a period of 8 months

Plant 3

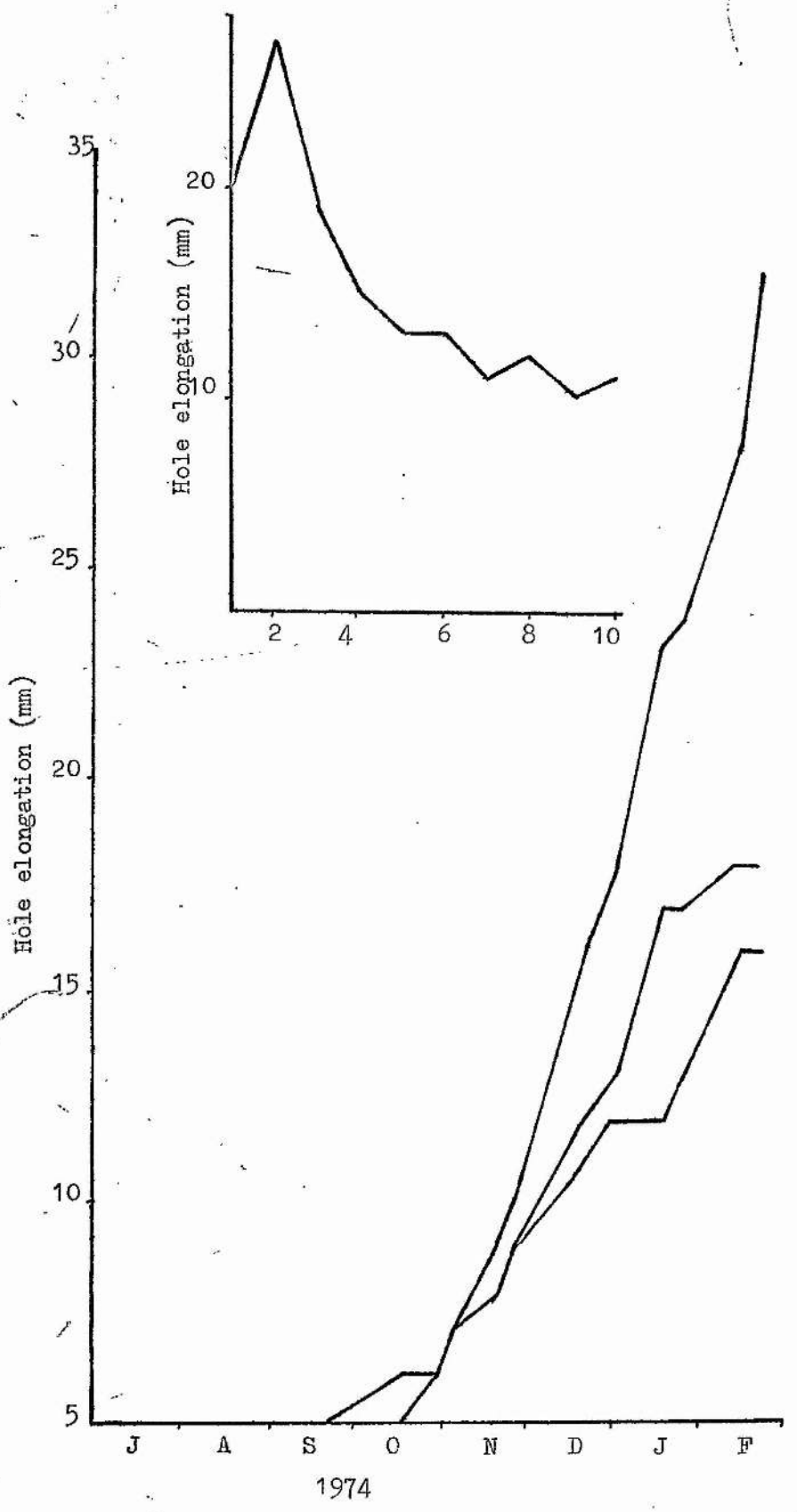

Fig. 5.5 Linear growth as indicated by hole elongation (mm) over 8 months

Inset as Fig. 5.1

Plant 4

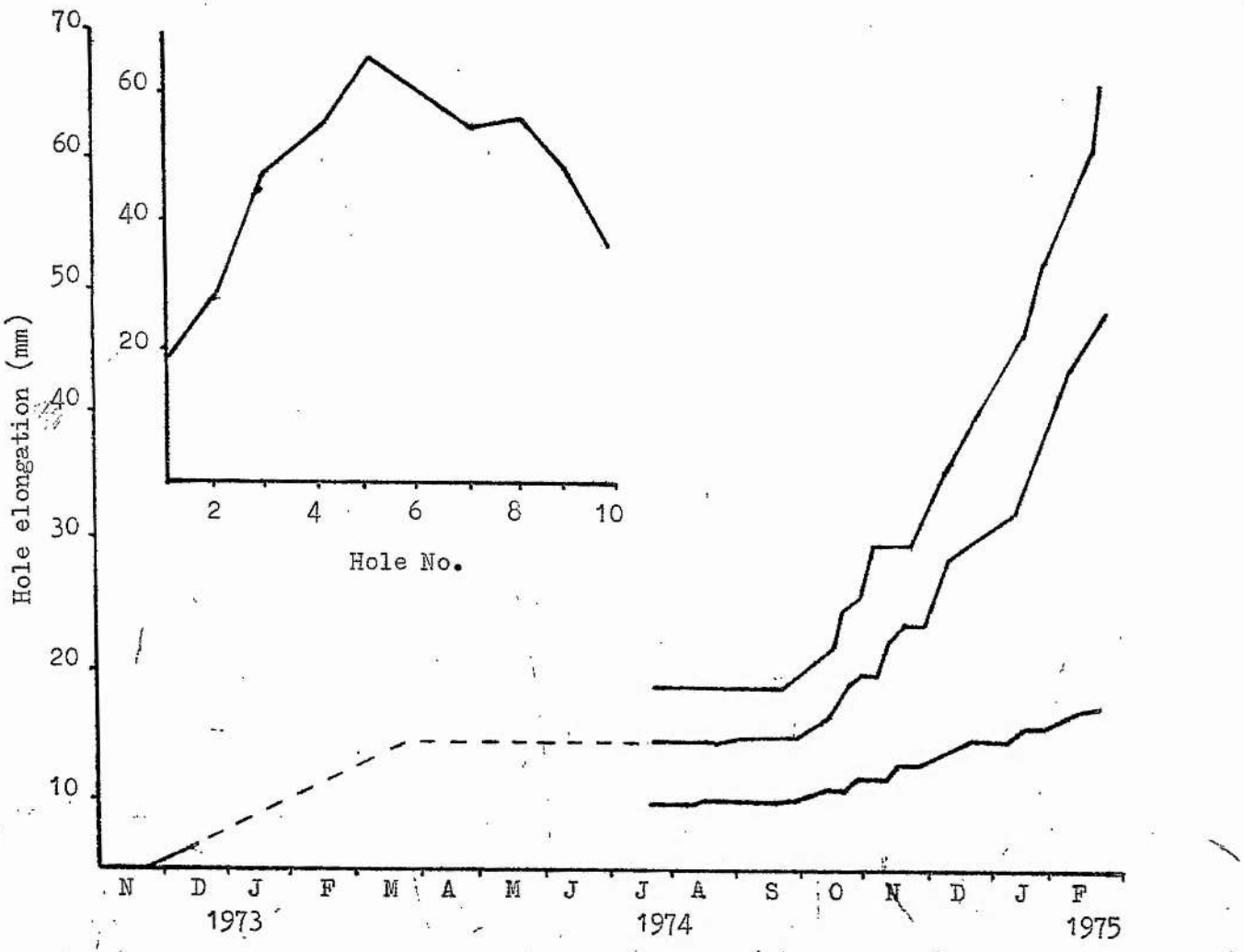

Fig. 5.6 Linear growth as indicated by hole elongation (mm) over 16 months. Dashed line indicates period when plant not measured over winter. Inset as in Fig. 5.1

Plant 5

not measured. It should be noted that by "elongation" of the punched holes, what is meant is the change in shape of the holes from a 5mm diameter circle originally to something resembling an elipse, often 50mm or more in length and 10mm or more in width. The elongation measured(Fig. 5.8) was parallel with the long axis of the lamina. Presented as an inset on each graph is a plot of the total elongation (over the period of the experiment) of each of the 10 holes in that particular lamina.

The graphs show the elongation of three of the 10 holes for each plant, including maximum, minimum and median. These three curves were drawn for the sake of clarity, to show the range of results and a mid-value. A family of 10 curves made interpretation difficult.

The general rhythm in the annual rate of elongation can be seen in plants 1 and 5. The rates of lamina growth, tabulated below were obtained by dividing the increase in length of the marked strip of lamina by the period of observation. Also shown in the table are details of the various habitats of the plants.

Plant	Length Increase(mm)	Time (Days)	Rate ($mm.wk^{-1}$)	Habitat
1	356	368	6.93	Exposed gully mouth
2a	237	289	5.74	Sheltered cliff base
2b	244	289	5.88	" " "
3	194	232	5.88	" gully centre
4	356	232	10.71	Partial shelter among boulders
5	686	450	10.64	Exposed cliff face
6	340	227	10.50	" rocky slope

Table 5.1 Variations in rates of growth of seven laminae in differing habitats at the shallow site, over varying periods of observation.

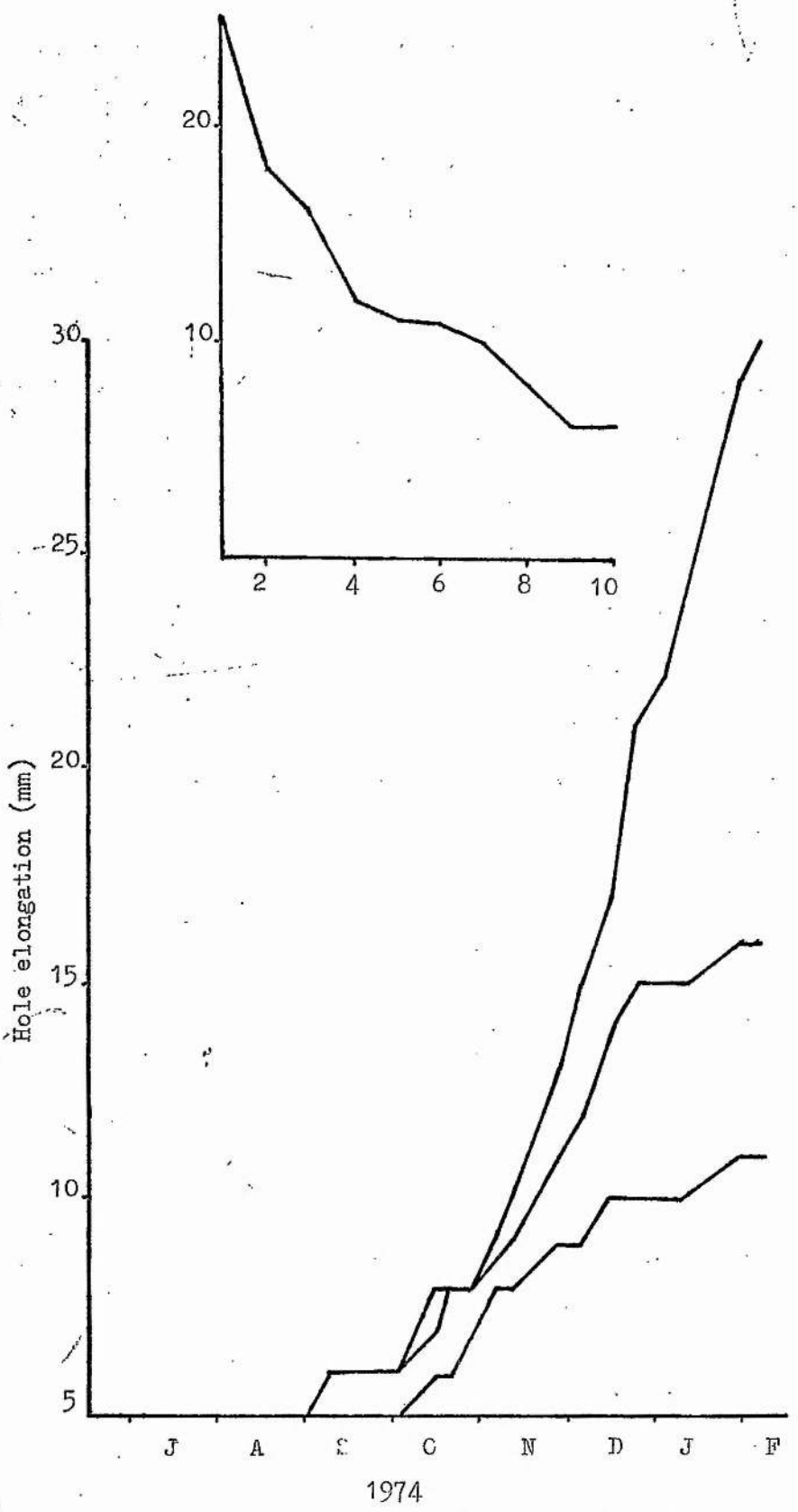

Fig. 5.7 Linear growth as indicated by hole elongation (mm) over a period of 8 months. Inset as Fig. 5.1

Plant 6

From table 5.1 it appears that there is some correlation between the rate of growth of the lamina and the degree of exposure.

All the graphs show that during the winter months from May to approximately mid-September there was no lamina growth. (See Table 5.3 for date of commencement of growth). The first sign of growth was the observation of new haptera on 23.9.74 on plant 3, growing in the centre of one of the rocky gullies. These are clearly visible in a photograph taken at the time (see Plate 3, Chapter 2 and Discussion for further details), occurring before any lamina elongation had taken place. Similar growth in other plants was not seen until late October, after the departure of the sea ice. A relatively steady rate of elongation was then observed for all of the plants over the remainder of the growing season until all were destroyed in the February 1975 storm.

Table 5.2 below shows how the elongation of the marked strip of lamina containing the 10 holes and the maximum observed elongation of a single hole varied between the different plants. Fig. 5.8 shows how the overall elongation of the marked strip was measured and the change in shape of the holes. Figures are given for both the 1974 growing season

Plant and Habitat		Summer 1974 Overall Elongation(mm)	Summer 1974 Max. Hole Elongation (mm)	Period of Experiment Overall Elongation(mm)	Period of Experiment Max. Hole Elongation(mm)
1	E	271	33	356	59
2a	S	152	14	237	21
2b	S	159	13	244	23
3	S	164	9	194	16
4	E/S	288	24	356	32
5	E	258	22	340	30
6	E	258	22	340	30

E – exposed habitat

S – sheltered habitat

E/S – partially sheltered

Table 5.2 Variation in the maximum hole elongation and overall elongation of the marked strip between plants. Data given for one summer (1974) and for the total period of observation (number of days as in Table 5.1). An indication of the habitat of the plant is included.

and the total period of the experiment.

Both of these tables appear to show some correlation between the habitat of the plant and its rate of elongation. The two laminae studied on plant 2, found at the base of a small cliff under an overhang show far less elongation than that of plant 6 growing in the centre of a rocky slope, a far more exposed and better illuminated position. Plant 3, in the most sheltered and shaded position of all, grew least, while plants 1 and 5 grew much more rapidly, being less shaded.

The time of initiation of growth did show some slight variation amongst the plants, as shown below, together with the increase in width of the laminae observed over the 1974 season.

Plant	Growth Initiation	Width Increase (mm)
1	Late August	91
2a	" September	22
2b	" "	18
3	Early October	24
4	Mid September	30
5	" "	50
6	" "	32

Table 5.3 The variation in commencement of growth in 1974 together with the lamina width increase observed for that season, in mm.

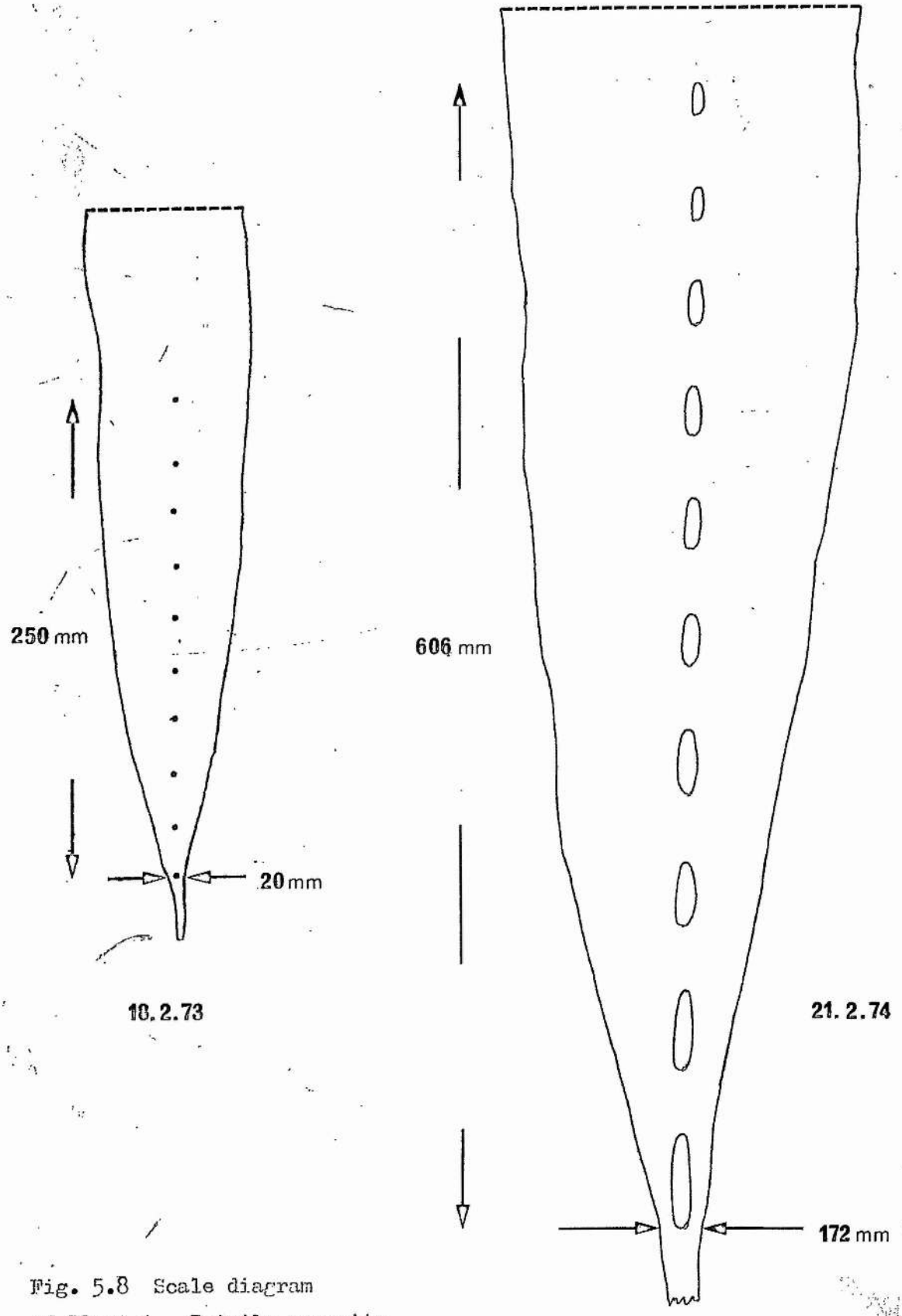

Fig. 5.8 Scale diagram
of Plant 1. Details opposite

Fig. 5.8 A scale diagram of Plant 1 at the beginning and end of the 368 day period of observation. The scale is 1/30 life size except for the initial lamina width of 20mm which for clarity is shown at 1/6 life size. Three measurements were made on each lamina: the width of the lamina at the first hole, the total length of the marked strip (both indicated by arrows) and the longitudinal length of each hole. The overall length of the lamina varied due to abrasion, and could not be measured accurately.

The width of the laminae showed a steady increase during the growing season, measured near the base of the lamina as shown in Fig. 5.8. This increase was generally 10–14% of the increase in length. Plant 1 was the only exception the width increase being 33.6% of the length increase.

Plant 5 best illustrates how the rate of elongation varied along the lamina. The dashed line in the graph indicates a period when the holes were not measured, as it was thought the plant had been destroyed, whereas it had been concealed by an adjacent Ascoseria plant and was later rediscovered. The first hole of the series was punched in stipe tissue which showed very little elongation. The next 3 holes, in tissue at the base of the lamina showed an increasing degree of elongation until the main region of elongation activity was reached. In the seven laminae observed in this experiment, this region was usually found between 40mm and 70mm from the base of the lamina. However only in plant 5 were holes punched before the meristem region and near to the stipe as this weakened the plant. All the other plants had their first holes in that region of the lamina which gave the maximum hole elongation; that of the other holes decreasing distally.

The contribution of the fastest elongating hole to the overall lamina elongation ranged from 9.8% to 21.6% and in all the laminae some elongation was observed before 30.10.74 when the sea ice blew out. Plant 1 appears to show some elongation in hole 1 during the early months of winter. It must be emphasised however that this seemingly anomalous observation is only an elongation of the order of 2mm over a 4-month period, mid-April to mid-July and could easily be accounted for by observer error. Certainly, more detailed work is needed before any conclusions can be drawn about lamina growth at that time of year. The 'steps' that appear in the graphs are a result of measuring only to the nearest mm, the greatest accuracy that could consistently be obtained by a diver in these cold conditions.

II LAMINA AREAS, GROWTH RATES OF YOUNG PLANTS AT THE SHALLOW SITE AND BIOMASS PER UNIT AREA

1. Lamina Areas

The total surface area of the laminae of Phyllogigas within the area mapped at the shallow site was measured. (For details of the map see Chapter 2). The following data were obtained:

Number of plants	=	39
Number of laminae measured	=	151
Total surface area laminae	=	$2.2m^2$
Area covered	=	$800m^2$
Mean dry weight $25cm^2$ samples	=	0.2840g
Specific Leaf Area (SLA)	=	$0.088cm^2.mg^{-1}$
Leaf Area Index (LAI)	=	$0.0028m^2$ lamina.m^{-2} sea bed

All the laminae measured showed signs of distal abrasion. The figure obtained for LAI is in marked contrast with that obtained at Cam Rock (Section II, part 3, this chapter) in a dense stand of Phyllogigas.

2. Growth rates of young plants

The four young plants with a total of 13 laminae, found at the shallow site on 29.1.75 were not recorded on the map made of the area the previous winter. From this it was assumed they were new growth of that season, over a period of three months. All the plants were growing on a cliff face in 3m of water. Their situation meant they could not have been there during the winter as they would have suffered complete abrasion by the ice. In such a position they were receiving maximum illumination. Table 5.4 below shows the parameters measured.

Plant	Max. Lamina Width(mm)	Lamina Length (mm)	Lamina Area (mm^2)	Long. Growth Rate ($mm.wk^{-1}$)	Total Area(mm^2)
A	100	198	19800	16.5	
	68	155	10540	10.3	
	94	170	15980	14.2	
	54	120	6840	10.0	52800
B	112	98	10976	8.2	
	144	98	14112	8.2	
	138	103	14214	8.6	
	146	118	17228	9.8	56530
C	172	90	15480	7.5	
	164	80	13120	6.7	
	170	120	20400	10.0	49000
D	110	115	12650	9.6	
	115	95	10925	7.9	23575

Table 5.4 Parameters measured in 13 laminae of four young plants on 29.1.75 after three months growth, in 3m depth at the shallow site.

The mean growth rate was found to be $9.8mm.wk^{-1}$, calculated from the data for lamina length. All these plants were destroyed in the February storm before any further data could be gathered.

3. Biomass per unit area

In most areas studied the plant distribution was very sparse and completely unsuited to measuring productivity by the increment cropping technique. Two areas of $1m^2$ were however cleared at Cam Rock during January 1973 at 6.5m depth and observed periodically over the next 27 months. During that time no recolonisation was observed except seven specimens of

Leptosarca simplex A. & E.S. Gepp, (this corresponds to Leptosomia simplex, a name applied in error by Kylin and widely used in recent papers on Antarctic algae (Drew, 1977)) growing on the remains of holdfasts of Ascoseia mirabilis Skottsb.

In February 1975 an area was cropped at Cam Rock in one of the denser 'stands' of Phyllogigas to obtain some idea of the biomass of that species there. The following data were obtained:

Area cleared	=	$8649 cm^2$
Number of laminae	=	27
Total lamina area	=	$39032 cm^2$
Mean lamina area	=	$1445.6 cm^2$
Total lamina fresh weight	=	3241g
Total lamina dry weight	=	703g
Dry weight as % fresh weight	=	21.69%
Biomass per unit area	=	$812.8 g.m^{-2}$
Specific Leaf Area (SLA)	=	$0.06 cm^2.mg^{-1}$
Leaf Area Index (LAI)	=	$4.5 m^2$ lamina.m^{-2} sea bed

III "TISSUE COMPOSITION"

1. Mannitol Content

Fig. 5.8 shows the seasonal variation in mannitol content over a 17-month period from September 1973 to January 1975, monitored at the shallow site. At first sight the curve appears very erratic but it can be split up into four distinct parts.

1. Two periods of low mannitol levels during the winter months.
2. Two periods of high levels during the summer months.

It should be noted however that these measurements were made on material used in in situ photosynthesis experiments, and not sampled with biochemical consistency too much in mind.

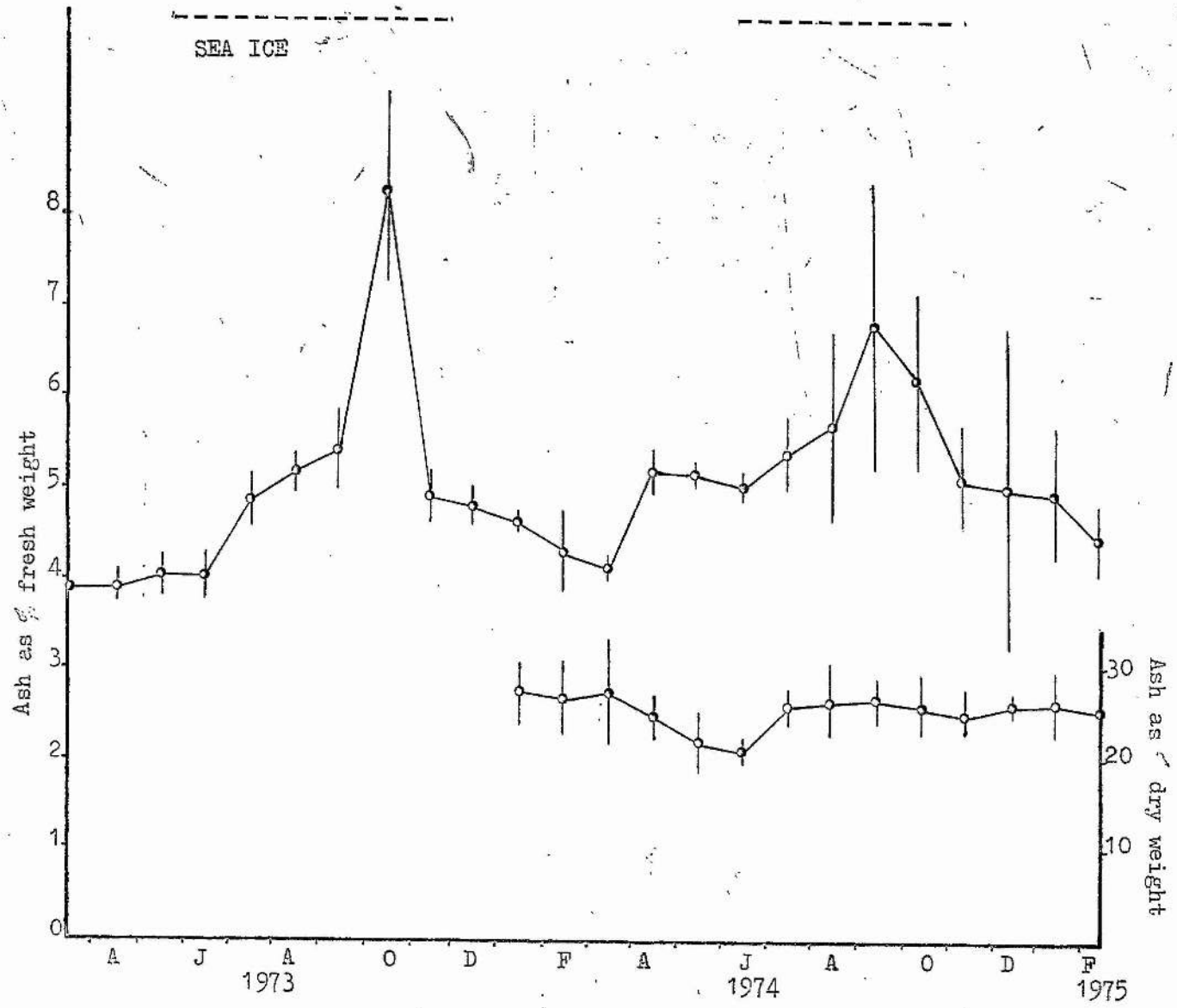

Fig. 5.9. Seasonal variation of ash content of frond.

A second curve shows the ash weight as % dry weight, from January 1974. The organic weight (dry weight - ash weight) was calculated over this period and similarly showed little variation:

Organic weight expressed as % dry weight

Maximum	78.8%	17.9.74
Minimum	72.5%	9.1.74
Mean	75.6% $\pm$ 2.1%	

(Monitored at the shallow site only)

The seasonal variation in the ash weight, expressed as % fresh weight is quite marked. The maxima occur in both cases about 6 weeks before the sea-ice broke out despite the time of the break out being 5 weeks earlier in 1974 than 1973. Why these maxima should occur when they do is not clear unless it is in some way correlated with the growth of reproductive structures. The standard deviation of the results is included.

The second curve, ash weight as a % of dry weight shows remarkably little variation. A low point in June is reached after a decline beginning in March, a trend partially mirrored in the mannitol levels, though more frequent sampling would have been useful here.

3. Calorific content laminae

Very little variation was shown in the samples analysed, covering a period of 13 months from January 1974 to February 1975. The following data were obtained:

Maximum	4.7 $kcal.g^{-1}$	on	13.11.74	at 4.8m depth
Minimum	3.4 $kcal.g^{-1}$		5. 7.74	6.2m depth
Mean	3.9 $\pm$ 0.002 $kcal.g^{-1}$			

This mean figure was used in the calculation of photosynthetic efficiencies.

CHAPTER 6

GENERAL DISCUSSION

I INTRODUCTION

Skottsberg (1906, 1941, 1953) has analysed the general characteristics of the marine vegetation in relation to the physical factors of the environment. In the later of these publications he considered the term elittoral to be best reserved for the belt completely devoid of benthic vegetation. Earlier, Kjellman (1877) had defined it as the region from a depth of 37m (the limit of his lower sub-littoral belt) down to the limit of attachment of macroscopic algae. This lower limit according to Zaneveld (1966) lies at the rather incredible depth of 668m in the Ross Sea. More will be said about this point later.

Of all aspects of plant metabolism, photosynthesis shows the most prominent variation under the dictates of the immediate environment (Talling, 1961). As near natural conditions as possible is an essential prerequisite of any attempt to measure the effect of environmental factors on photosynthetic rates of marine algae. Once such data has been obtained it is then possible to assess how important photosynthesis is during the growth period of the plant.

The unique value of aquatic plants for illustrating photosynthetic processes was first realised in the 1920's by marine and freshwater biologists, e.g. Gail (1922), Ruttner (1926), Gaarder & Gran (1927) and Marshall & Orr (1928). Gail, for example, determined the maximum level

of photosynthesis, by *in situ* measurements of some red and brown sub-littoral algae and related his data to depth and light. The maximum amount of photosynthesis of the brown algae occurred at a depth of 1-8m whilst that of the red occurred at 10-25m. Both depths were decreased by cloudy weather or choppy water. Tikhovskaya (1940) showed that photosynthesis of *Laminaria saccharina* changed markedly with depth and season and that growth could still take place during the polar night in December and January when no photosynthesis occurred. Sargent and Lantrip (1952) working with *Macrocystis pyrifera* and using *in situ* measurements of photosynthesis showed the necessity of translocation to supply organic material to the growing tips of the plant which were found to be below the compensation point. Blinks (1951, 1955) and Kanwisher (1966) report on the photosynthetic rates of littoral and sub-littoral algae in various ecological situations while Printz (1939), Levring (1947, 1966, 1967) and Drew (1969b) have, in the process of studying the zonation of sub-littoral algae, carried out *in situ* measurements of photosynthesis in several genera. There have been extensive studies on the productivity of marine phytoplankton, reviewed by Strickland (1958), using both the Winkler oxygen technique and the ^{14}C technique devised by Steemann-Nielsen (1952).

Regarding the macroalgae, once *in situ* studies of photosynthesis such as those mentioned above have been made it is possible to assess the importance of photosynthesis during the growth period of the plant. Neushul (1963) suggested that aphotic conditions existed under thick ice cover, but later work of Zaneveld (1966) disproved this. He found that 1.4% of incident light, i.e. a calculated 13 foot-candles penetrated to a depth of 20m under a 2m thick ice cover with only a trace of snow. It should be emphasised that there was only a trace of snow overlying the

ice at that time; the amount of light penetrating the ice is strongly dependant on the state of the ice surface which may be overlain by snow or melt ponds, saturated with melt water, drained or polished by the wind (Maykut & Untersteiner, 1971). Only long term studies involving in situ measurements of photosynthesis can determine the effects of such variable environmental factors.

II PHOTOSYNTHESIS AND RESPIRATION -- AN ASSESSMENT OF THE METHODS USED

A. In situ photosynthesis

The ^{14}C method was used to measure in situ photosynthesis in Phyllogigas throughout the year, at various sites; the advantages and disadvantages of this method are set out below.

Advantages

1. The algal tissue suffers minimal disturbance from its natural environment. The effect on the plants of their removal to the laboratory is not known but it seems likely that there would be some effect. Kanwisher (1966) reported a decrease in oxygen uptake of samples stored in the laboratory, in the light.

2. The difficulties of simulating the complexities of the marine environment are removed and the photosynthesis of the algae under various natural conditions can be measured. A review by Strickland (1958) considers the problems of incubators and the simulation of underwater light.

3. The apparatus allows a broad spectrum of experiments to be carried out; measurements of shading, growth and recolonisation can be made. Algae of unknown age and those unsuitable for increment cropping can be studied with this technique.

Disadvantages

1. Obtaining adequate replication can be a problem.

2. With large surface area: volume ratios of the tissue discs, the formation of nutrient-poor diffusion shells may occur. Adequate circulation of the bathing solution is necessary to prevent stratification of boundary layers. (Whitford & Schumacher, 1961).

3. Quantitative estimations of the effect of environmental variables on photosynthesis, with the exception of the 'key' factor of light (Talling, 1961) are difficult.

No mechanical stirring of the incubation medium was incorporated into the method used, but the low tissue: volume ratio together with the movement of the platform should have kept nutrient depletion to a minimum.

Interpretation of in situ ^{14}C experiments

Since Steemann-Nielsen first introduced the ^{14}C technique for measuring primary productivity in 1952, it has been widely used in marine studies. Its main advantage over the more traditional oxygen exchange methods is its much greater sensitivity. However, there have been doubts expressed as to what exactly the uptake of ^{14}C measures. Ryther (1954, 1957) believes it to be net photosynthesis while Steemann-Nielsen and Hansen (1959) are of the opinion that an intermediate value, between net and gross, is measured. These differing views are summarised by Fogg (1963) who also mentions the exudation of organic compounds by marine algae as an important contribution to the carbon content of seawater. (See also Sieburth, 1969). Rodhe (1958) held that short-term experiments measured an intermediate value between net and gross photosynthesis. Fogg (1963) conducted simultaneous experiments on Anabaena using ^{14}C and Winkler techniques and by comparison found that ^{14}C measured gross photo-synthesis. Saunders (1964) considered gross photosynthesis to be measured

in short-term experiments and Jupp (1972) conducted an *in situ* experiment where ^{14}C and Winkler measurements of photosynthesis were made simultaneously. He found a close correlation between the value for gross photosynthesis from the Winkler results and those from the ^{14}C method.

Assuming ^{14}C uptake to be a measure of gross photosynthesis the following conditions have to be met:

1. The plant is able to take up the ^{14}C offered rapidly.
2. There is no isotopic discrimination against ^{14}C.
3. The losses of ^{14}C through respiration during an experiment are negligible.
4. The losses of ^{14}C as a result of exudation of labelled organic compounds, e.g. carbohydrates, are negligible.

These points will now be considered in turn.

1. The nature of the ^{14}C offered

The ^{14}C used in these experiments was in the form of sodium bicarbonate for the following reasons.

The buffering action of the carbonic acid system in seawater ensures that its pH remains fairly constant over the range 7.8 - 8.3 (Skirrow, 1965). At this range over 90% of the inorganic carbon is in solution as the bicarbonate ion, HCO_3^-. The literature contains little on the merits (or otherwise) of various carbon sources for photosynthesis in macrophytic algae but the existance of a light-stimulated pump for HCO_3^- ions has been demonstrated in the freshwater alga *Hydrodictyon africanum* by Raven (1968). Joliffe & Tregunna (1970) observed the effect on photosynthesis of varying pCO_2 and inorganic carbon (supplied as bicarbonate) on various algae. The '*Ulva*' types (including *Laminaria* here) were unaffected by changes of pH or pCO_2 but photosynthesis was seen to be

dependant on the concentration of inorganic carbon. From this they concluded that these plants used bicarbonate as their major source of carbon.

2. Isotopic discrimination

Despite the extensive use of ^{14}C labelled compounds in photosynthesis studies, there is no general agreement on the extent to which isotopic discrimination occurs in mixtures of ^{12}C and ^{14}C. High values of about 15% discrimination against $^{14}CO_2$, reported by Weigl & Calvin (1948) and by Van Norman & Brown (1952) depended upon the assumption that the respiratory release of $^{12}CO_2$ continued in the light; the apparent agreement between their estimates is largely fortuitous since different respiratory corrections were applied. On the basis of his estimates of ^{14}C release in the light Steemann-Nielsen recalculated some of the earlier data and obtained lower values of 5% discrimination. It is evident that all of these estimates are very dependent upon the assumptions made concerning the release of CO_2 in the light, (Yemm & Bidwell, 1969). These latter authors found discrimination against ^{14}C to be as low as 2% as long as there is little or no evolution of CO_2 during irradiation. In view of this low value, lack of general agreement in the literature and the absence of suitable apparatus to monitor CO_2 evolution in the field, no discrimination correction factor was applied in this work.

3. Respiration losses

In this work it has been assumed that the repiration rate in the light is the same as that in the dark. Moderate light intensities did not affect the uptake of oxygen by Chlorella (Brown, 1953), but it is now recognised that respiration and photosynthesis are unlikely to work

independantly, and photorespiration may replace dark respiration (Hoch, Owens & Kok, 1963). See Jackson & Volk (1970) for an interesting review of the problem of photorespiration. Jupp (1972) examined the effect of light on the evolution of respiratory CO_2 from labelled substrates and showed that over a 4-hour period (the usual duration of a ^{14}C experiment) the loss of previously fixed ^{14}C as a result of respiration was very small.

This suggests that little ^{14}C-labelled products reach the respiratory centres - the mitochandria - during the short time period involved and of the small amount of ^{14}C respired, little is refixed. Some storage of labelled products may occur. The uptake of the isotope during in situ experiments is considered to represent gross photosynthesis insofar as respiratory loss is concerned. A correction of 6% was applied by Steemann-Nielsen (1955) for respiratory loss and refixation in phytoplankton. According to Ryther (1954), complete refixation of fixed ^{14}C would mean ^{14}C uptake measures net photosynthesis, but from the data of Steemann Nielsen (1955) and Jupp (1972), less than complete refixation occurs. At lower light intensities the diffusion gradients of carbon into the chloroplasts may be smaller as a result of lower photosynthetic rates thus in turn lowering the refixation rates.

4. Exudation losses

Unlike certain species of Laminaria, Phyllogigas does not appear to produce mucilage and therefore no experiments were carried out to determine what if any were the exudation losses of organic compounds. It is assumed that the major compound labelled during photosynthesis, mannitol, is either stored in the vacule or redistributed throughout the plant. Sieburth (1969) has shown that considerable amounts of carbon may be

exuded by macrophytic algae - up to 40% of the net carbon fixed by L. agardhii and L. digitata, but nothing is known in this respect about Phyllogigas.

B. Respiration using the Winkler technique

The Winkler method was used to measure the dark respiration rate of Phyllogigas tissue in the laboratory throughout the year. This technique is considered by many to be the most reliable and precise means of analysing dissolved oxygen in seawater. Strickland & Parsons (1965) have reported the method to be precise to within $\pm$ 0.5% at the 0.7mg atoms. l^{-1} level.

Advantages

1. Relatively easy to replicate results.

2. Easy to study quantitatively the effects of envionmental variables such as temperature and salinity.

3. High precision attainable.

Disadvantages

1. Damage to tissue is unavoidable in the collection of samples.

2. Short-term experiments are necessary to keep errors associated with incubation to a minimum.

3. Reduced circulation of the bathing solution may produce nutrient-poor diffusion shells around tissue.

4. Only approximate simulations of the natural environment can be made and variables can only be considered singly.

Some of these disadvantages will now be considered in greater detail.

1. Tissue damage

The cutting of small discs to measure their metabolic activity may affect the very rates it is desired to measure. Significant errors have been caused in this way to the measurement of the respiratory rate of Grateloupia while Padina, under the same conditions was unaffected. (UNESCO, 1973).

2. Incubation errors

To minimise the errors associated with incubation listed here, short time periods were used. However, the time involved in manipulation, addition of reagents etc., can then become an increasingly significant source of error.

3. Boundary layer effects

The effects of inadequate circulation of the bathing medium have already been considered in Chapter 3.

4. Simulation of the marine environment

The difficulties of attempting this hardly need elaboration here; the problems involved in attempting to quantify the effects of several variables continually in a state of flux have been considered by Strickland (1958).

III DISCUSSION OF RESULTS

Productivity studies in Antarctic waters have tended to concentrate on the phytoplankton. The results obtained in this study will, therefore, be compared with those obtained from similar studies of algae in more temperate waters around the coasts of the U.K. and in the cooler waters of the coasts of Norway and Canada. The table below gives a summary of the biometric and growth parameters in Phyllogigas grandifolius.

PARAMETER	UNITS	
Net annual primary productivity	metric tons.hectare^{-1}.year^{-1}	15.3
Growing season mean productivity	gC.m^{-2}sea bed.day^{-1}	2.4
Biomass	kg.m^{-2} sea bed	0.813
Mean LAI	m^2 lamina.m^{-2} sea bed	4.5
Gross photosynthesis	ugC.cm^{-2} lamina.h^{-1}	6.7
Net photosynthesis	ugC.cm^{-2} lamina.h^{-1}	5.15
Photosynthetic efficiency	total irradiance	Winter 1 Summer 14%
Respiration	ugC.cm^{-2} lamina.h^{-1}	1.55
SLA	cm^2.mg^{-1}	0.075
Mean growth rate	mm.wk^{-1}	8.0

Table 6.1 A summary of the biological data obtained in this work, with respective units, of Phyllogigas grandifolius.

The photosynthesis and respiration data will now be considered in detail, comparing results where possible with those for L. hyperborea, the dominant member of the sub-littoral kelp forest ecosystem in temperate waters around the U.K. coasts.

Figs. 4.1a and b and 4.2a and b show the seasonal variation in gross and net photosynthesis at the two sites. Clearly only one maximum per season was seen. In Table 6.2 below it is apparent that the maximum values of net photosynthesis recorded for the deeper of the two sites occurred later than at the shallow site and were smaller.

	SHALLOW SITE		DEEP SITE	
	Date of Max.	ugC.cm^{-2}.h^{-1}	Date of Max.	ugC.cm^{-2}.h^{-1}
1973	early Dec.	3.6	mid Dec.	3.0
1974	early Nov.	5.2	late Nov.	4.0

Table 6.2 Variation in date and quantity of maximum observed value of net photosynthesis at two sites, 6.2m and 10.8m, over two consecutive seasons.

Jupp (1972) records maximum values in May for L. hyperborea, much later in the growing season than Phyllogigas and with not such an abrupt transition from winter levels. Approximate values are given below for net photosynthesis:

March	5.3	ugC.cm^{-2}.h^{-1}
April	9.1	"
May	13.8	"

with a decline in June (mid-summer) and negative values in July (Taken at 3.1m).

Negative values of net photosynthesis for Phyllogigas were only observed towards the end of the 1973 winter (again later at the deeper site), indicating that the plants at both sites were below compensation point and consequently, suffering from a loss of carbon as a result of respiration. This occurred even though the respiration rate at the shallow site at this time was at its lowest level, 1.6 to 1.8 $ugC.cm^{-2}.h^{-1}$. (see Fig. 4.3). Winter respiration levels in L. hyperborea were much higher; 14.0 $ugC.cm^{-2}.h^{-1}$ (February) and 12.0 $ugC.cm^{-2}.h^{-1}$ (November) (Jupp, 1972). The water temperature in Borge Bay at this time was $-1.7^{\circ}C$ at the end of September when the net photosynthesis 'went positive' at the shallow site and $-1.76^{\circ}C$ at the deep site which 'went positive' 1½ months later, in mid-November. (Data from Fig. 2.1).

The curves for daily accretion, Figs. 4.1c and 4.2c show similar characteristics. Positive accretion, expressed in $ugC.cm^{-2}.d^{-1}$ was observed only during the summer months, and it can be seen that 1974 was the better season in that it produced a higher summer maximum at both sites than in 1973. (See Table 6.2, below). Readings for the remainder of the 1974/75 summer were halted by the effects of a severe and prolonged storm in February which effectively destroyed both the sampling sites and did extensive damage to the sub-littoral communities in Borge Bay.

	SHALLOW SITE D.A. ($ugC.cm^{-2}.d^{-1}$)	DEEP SITE D.A. ($ugC.cm^{-2}.d^{-1}$)
1973	55	45
1974	70	56

Table 6.3 Variation in magnitude during two consecutive seasons of maximum observed value of Daily Accretion, (D.A.); dates of maxima as in Table 6.1.

The daily accretion curve for 1973 at the shallow site shows a steady increase while the sea-ice was still present, rising from 7 to 45 ugC. cm^{-2}. d^{-1} during the month of November then dropping sharply and rising again to the maximum value of 55 ugC. cm^{-2}. d^{-1} in early December. This variation may be explained as follows:

In the latter half of November, the sea-ice over the whole of Factory Cove became increasingly thin. With the absence of any snow cover, melting could proceed from both above and below, and the ice became more and more transparent to light. Evidence of this was seen as the ice became apparently darker in colour, a result of the transmission of previously reflected light into the water beneath. This would appear to account for the increase in the rate of daily accretion in the latter half of November.

In February, the equivalent period in the growing season of L. hyperborea, Jupp (1972) showed photosynthesis to be negligible and a low photosynthesis: respiration ratio to exist. He demonstrated that translocation of reserves from the old lamina was assisting the early growth of the new lamina. Translocation was not shown to occur in Phyllogigas; but as growth appears to be more generalised throughout the lamina than in the Laminarias, this would not be expected to be as important. More work is needed on this aspect.

The drop in daily accretion in late November and early December was probably caused by turbulence associated with the break-out of the ice. Once the ice had gone, and the water cleared, the phytoplankton immediately started to bloom, explaining why the maximum value in 1973 was lower than in 1974. The phytoplankton bloom started in early December each year, possibly being triggered by day-length (Whittaker, pers. comm.), so that when the ice blew out at the end of October 1974, the macroalgae had

optimum growth conditions for nearly a month; high light levels and clear water leading to the production of a burst of growth observed in the in situ growth experiment. Why this daily accretion rate should drop so rapidly in November when there was very little phytoplankton present and the results of the in situ growth experiment show a continued increase in growth, is hard to say. Perhaps the discrepancy might be accounted for by physiological differences between the plants used in the two series of experiments. The incident light levels at the surface were high: 9.9 kcal. cm^{-2} for the month, the water temperature rose rapidly during the latter half of the month and was recorded as $+0.6^{\circ}C$. in the early half of December. The phytoplankton chlorophyll levels only began increasing in December 1974 as can be seen from the curve in Fig. 2.8 and day-length was a little over 17 hours (Fig. 2.4). Light inhibition appears unlikely; the only explanation that can be offered at present is that increased turbulence of the water body stirred up the layer of diatoms lying at the substrate-water interface, deposited from the ice at break-out, thus reducing the amount of light available to the plants. The final summer's work was brought to an untimely conclusion before any further information could be gathered about the high value of daily accretion observed in January 1975.

B. Late Summer and Winter

The daily accretion was negative well before the formation of the sea-ice, at both sites in 1974, even allowing for the effects of the February storm. This would imply that other factors apart from the presence of sea-ice limit the growing season towards the end of summer. The ice, as was seen in 1973, can however extend 'winter' conditions right into December and so plays an important role in limiting the growing season at the beginning of summer. Daylength at the end of February is 14.1 hours and the water

temperature +0.2°C dropping to below zero from the beginning of April to the end of November in 1974. Daily accretion remained negative from the end of February to early October at the shallow site, when daylength is once again just greater than 14 hours. Perhaps undue emphasis is being placed on daylength as a limiting factor in this case, but as has been pointed out, some close correlations can be drawn. Further studies are needed on this topic.

C. The Deep Site

For the deeper of the two sites, the picture is essentially the same, though with less detail due to the lower sampling frequency. Both summer maxima appear well after the departure of the sea-ice, particularly in 1974: nearly 3 weeks later (Figs. 4.2b &4.2c) , net photosynthesis and daily accretion). There is also a secondary peak in February 1974, later than the equivalent peak at the shallow site, and again, smaller. As Luning (1970) remarks, it seems reasonable to suggest that underwater irradiance rises to levels necessary for lamina growth later at the deeper site. These secondary peaks at both sites appear to be due to the water clearing again after the phytoplankton bloom, though the very abrupt drop observed in March at the shallow site was caused, as previously mentioned by another February storm disturbing the sediments in Factory Cove. This was not shown on the deep site curve due to less frequent sampling though it probably occurred. Negative values were again confined to winter months, probably for a longer period than shown and certainly for as long as at the shallow site; late February to early October. The levels of daily accretion recorded are not as low as at the shallow site, though again, a greater sampling frequency during the winter months might have shown lower values to exist. A considerable increase in daily accretion for January 1975 was

again observed.

Jupp (1972) showed that as in Phyllogigas in this study, high values for lamina photosynthesis in L. hyperborea could be correlated with season. Positive net photosynthesis was first observed in spring (March) peaking in early summer (May) before maximum daylength unlike Phyllogigas. Drew (1972) also demonstrated that summer (June, July) photosynthesis in L. hyperborea was lower than that in spring, with negative values for net photosynthesis being recorded by Jupp (1972) in July, for which no explanation could be put forward. This pattern of seasonal variation of photosynthesis is very different to that observed in Phyllogigas. Both species are however below compensation point during the winter months. Several workers have noted that reduced summer photosynthesis occurred when temperatures were at a maximum and nutrients were at their lowest values: Tikhovskaya (1940), Black (1949), Black & Dewar (1949), Gessner (1955), Tseng et al (1957). From the small range of temperatures involved in this work, it would appear unlikely that it has any significant effect on the photosynthesis of Phyllogigas in situ.

The photosynthetic capacity of Phyllogigas, estimated on this work is low, when compared with data for other terrestrial and sub-littoral species. The table overleaf shows the net photosynthesis of various species under natural conditions.

Species	Light $cal.cm^{-2}.h^{-1}$	Temperature ^{o}C	NET PHS $ugC.cm^{-2}.h^{-1}$	Author
Pyrus malus	Natural	NS	54.6	Spector(1956)
Vicia faba	"	"	46.4	"
Pinus taeda	"	"	34.0	"
Solanum tuberosum	25.2	"	1.4	Chapman & Loomis in Thomas(1955)
Macrocystis pyrifera	Natural	15	39.6	Clendenning & Sargent(1957)
Saccorhiza polyschides	5.1	13.1	15.8	Jupp (1972)
L. hyperborea	6.2	8.8	13.3	"
L. saccharina	Natural	9.6	13.8	"
P. grandifolius	"	-0.5	5.2	this work
"	12.93	15.0	14.0	Drew (1977)

Table 6.4 Net photosynthesis under natural conditions

It can be seen that the photosynthesis of sub-littoral macrophytes compares favourably with other species (See Drew, 1977) for further work on Antarctic macrophytes). This is probably due to the high photosynthetic efficiencies and light-trapping ability of the kelps. The high photosynthesis of Macrocystis pyrifera and its high photosynthesis: respiration ratios (20 to 40, Clendenning & Sargent, 1957) indicate a high productive capacity in this species. Clendenning (1961) after a careful search of the literature states that laminae of Macrocystis can elongate faster than any other plant on land or sea on which there is information, attaining lengths of over 30m (100ft) in less than a year.

Drew (1977) compares the net photosynthesis values of Phyllogigas with his own data for L. hyperborea using winter material and an oxygen

method of determining the data and found a close similarity. He points out that the ^{14}C method, as used in this work gives consistently higher results often nearly twice the value of figures obtained by Winkler techniques (Drew, unpublished data).

Healey (1972) showed the optimum temperature for photosynthesis in Arctic seaweeds to be between 20 and 25°C but he considers them to be temperate rather than polar species.

D. An assessment of the hypothesis of heterotrophic nutrition

Wilce (1967) has suggested facultative heterotrophy as a means by which deep growing, attached, perennial high arctic marine algae adapt to their environment. This hypothesis has been shown to be untenable by Jackson (1971). However it was shown that the light requirements for photosynthesis could be reduced by an exogenous supply of glucose.

Heterotrophy appears unnecessary to support the growth of Antarctic algae, which although slow growing, may survive purely by their own photosynthesis. Data taken from the results and presented below enable approximate calculations to be made of the annual carbon balance of Phyllogigas.

Assuming a mean annual respiration rate of 2.00 ugC. cm^{-2}. h^{-1}, the amount of carbon lost through respiration in one year is

$$\frac{2.00 \cdot \ 24. \ 365. \ 10^4}{10^6} = 175.2 \text{ gC. } m^{-2}. \text{ yr}^{-1}$$

(Assuming the total area is covered by the tissue)

The mean annual sea temperature during the period of study was -0.7°C; during the winter months, May to November 1973 and July to November 1974 the temperature was steady at about -1.7°C (Fig. 5.1). This winter

temperature is the same as that recorded all the year round by Grainger (1959) and Lee (1966) in the high arctic. The respiration of Phyllogigas at these temperatures is shown in Chapter 3 part II. Kanwisher (1966) working on Laminaria populations in Labrador has suggested winter domancy in Arctic marine plants, whereas Kjellmann (1877, 1883) working in Spitzbergen and Siberia observed reproductive growth in winter, suggesting metabolic activity. Zaneveld (1968) working in the Ross Sea, Antarctica, records the collection by SCUBA divers of fresh fractifying specimens from under ice during the austral winter of 1967. Reproductive structures have also been observed in Phyllogigas in the latter months of winter.

The annual photosynthesis of Phyllogigas is shown in Chapter 3 part I. For the purposes of this calculation an average rate of gross photosynthesis of 4.00 ugC. cm^{-2}. h^{-1} is assumed, which is, if anything a little high. The respiration rate in turn could also be a little lower but in the final analysis, this does not appear to make a great deal of difference.

$$\text{Annual rate of photosynthesis} = \frac{4.00 \cdot 11 \cdot 365 \cdot 10^4}{10^6}$$

$$= 160.6 \text{ gC. } m^{-2} \cdot yr^{-1}$$

This figure is close enough to that of respiratory losses, given the approximations involved to show that heterotrophy is unnecessary in Phyllogigas grandifolius even during a severe winter. The alga, with a slow growth rate can survive purely by autotrophic means.

Zaneveld (1968) concludes that apart from the limitations imposed by the various substrates, the occurrence of elittoral macroscopic algae in the Antarctic does not need to be explained by a heterotrophic mode of nutrition.

E. Light and primary production – The Photic Zone Controversy

Light provides the energy necessary for the transformation of inorganic matter into organic matter by the algae. It is only the light absorbed by the pigments active in photosynthesis that is used for this transformation: generally only a part of submarine light.

In the photic layers of most areas of the seas the replenishment of the nutrient salts containing nitrate and phosphate is the essential factor determining the magnitude of the annual plankton primary productivity. However, in the polar seas this nutrient replenishment seldom limits the size of the primary productivity.

The annual variations in the rate of primary productivity in medium and high latitudes are largely due to annual variations in intensity of illumination (Steemann-Nielsen, 1974). Although measurements in quanta are theoretically the correct method of presenting the illumination rate in connection with photosynthesis, the use of energy units gives nearly the same results.

The intensity and quality of light reaching the chloroplasts of the algae depends on the optics of the water and on incident light reaching the sea surface, both of which must be considered in order to understand primary productivity. Only a part, 40%, of the solar radiation corresponding roughly to the visible part can be used for photosynthesis. The intensity of the solar radiation received at the surface of the sea varies with the latitude season, time of day and cloudiness.

The annual totals at high and low latitudes are not so different as is often thought. According to Kimball (1935) at Fairbanks, Alaska (65°N) it is about 50% of that at Miami (26°N).

Whereas seasonal variation in the tropics is insignificant, it is very large at high latitudes. According to Kimball again the average daily

insolation during the week that includes winter solstice at Miami is 55% of that during the week including summer solstice, whereas at Fairbanks it is only 0.8%. (Signy Island, 60°S: 2.8%; average of 1972, '73 and '74). Generally photosynthesis and respiration per 24 hours compensate each other at a depth where about 1% of the surface light occurs. This is the lower limit of the photic or photosynthetic zone and has been shown to occur at about 10m in summer at Signy Island (Horne et al., 1969). This depth, or compensation point occurs at 120m in the Sargasso Sea. (Sverdrup et al., 1942). Steemann-Nielsen and Jensen (1957) however defined the compensation depth as the depth at which the sum of the blue and green light is equal to 1% of the sum measured at the surface. In coastal waters often only the green part of the light is considered.

At the very low temperatures found in the Antarctic seas algae must be able to grow at much lower illumination intensities than ordinarily (Pechlaner, 1971). At least down to intensities of 0.015–0.03 $mW.cm^{-2}$ photosynthesis per day may equal respiration per day (Bunt, according to Allen, 1971). Drew (1977) quotes Compensation irradiance and depth of a number of Antarctic algae, among them Phyllogigas, with a compensation irradiance of 0.6 $mW.cm^{-2}$ at a depth of 7.7m. These figures are a long way short of the lower limit postulated by Zaneveld (1966) of 668m in the Ross Sea. Jerlov and Koczy (1951) found 0.0000001% of surface irradiance at 600m representing only 4×10^{-5} $mW.cm^{-2}$ on the sunniest possible day whereas Drew (1977) found the lowest compensation irradiances to be around 2×10^{-1} $mW.cm^{-2}$. Zaneveld (1968) said that transportation on the undersurface of icebergs may account for much of the material he collected.

Continuous 48 hour light intensity measurements by Zaneveld (1966) indicated an average scale reading of 53u amp in algal beds at a depth of 20m under a 26m thick layer of ice, ie. 1.39% of incident light. These

algal beds were found no further than 3km offshore from the Balleny Islands, Antarctica; coastal regions where the water is likely to be turbid.

Clarke (1966) reports that daylight was detected at depths as great as 800m in the Pacific and Indian Oceans.

It must not be overlooked that for a period of about 8 months temperature and light intensity are continuously very low. Low light intensity, low temperature and high hydrostatic pressure are known to reduce the rate of algal metabolism either directly or indirectly. According to Printz (1939) respiration in algae is affected principally by decreasing temperatures leading to an increase inthe ratio of assimilation to respiration and hence an assimilation surplus. This might make the survival of algae possible in the elittoral region during the austral winter period.

F. Growth of laminae

The seaweeds of the shore and shallow seas are a unique form of life (Mann, 1973) and their growth, below low tide level in the sub-littoral is far richer than in the intertidal areas. Before the use of SCUBA became so widespread, much work was done on the algae of the intertidal zone. (Lewis, 1964; Stephenson & Stephenson, 1972). While this zone is dominated by the fucoids, the sub-littoral is dominated by the laminarians, flourishing from low-tide level to a depth of 20 to 30m in clear water. Wave action keeps the blades in motion, providing the maximum exposure to sunlight and contact with nutrients. Under these favourable conditions growth may be very rapid, e.g. Macrocystis pyrifera with a rate of increase of frond (consisting of blades and stipe) of 2000mm. week^{-1} (North 1971) see also Aleem (1956); Neushul (1959); Neushul & Haxo (1963a). Other values include:

Laminaria saccharina (Parke, 1948)	121mm.wk^{-1}
L. hyperborea (Kain, 1976a)	66mm.wk^{-1}
L. angustata var. longissima (Kawashima, 1972)	250mm.wk^{-1}
Saccorhiza polyschides (Norton & Burrows, 1969a)	47–145mm.wk^{-1}

Numerous experiments on the growth of macrophytic algae have been carried out. Much of the earlier work on the Laminariaceae is contained in Fritsch (1945). Two Russian papers, not listed by him give some detailed information on the growth of L. saccharina in northern waters: Kireeva & Schapova (1933) and Tikhovskaya (1940) deal with the seasonal variation of this species in the Kola Fjord and the Barents Sea, working from size and weight variations throughout the year.

In L. hyperborea, lamina growth is known to be an annual phenomenon, with an abrupt transition between one season's growth and the next. In Phyllogigas as in L. ochroleuca and L. digitata the different seasons' growth are not so easily distinguishable and accurate estimates of lamina production can only be made by precise marking and increment cropping techniques. (Parke, 1948; Tseng, Wu & Sun, 1957; Sundene, 1964; Bellamy & Whittick, 1968; Mann, 1973). For comparing populations from different areas, John (1969) suggests the use of the stipe standing crop instead of the lamina as the large seasonal fluctuations in its ash content might be out of phase in different areas. The hapteron is rejected due to difficulty of sampling. Stipe standing crop (or any cropping technique) was unsuitable in Phyllogigas in the areas studied due to the widely scattered nature of the population and its slow recolonisation. Also the stipe showed no clear differentiation from the lamina.

Phyllogigas does not grow through the winter months unlike L. longicruris for example, which has been shown to grow rapidly throughout the

winter in eastern Canada, despite temperatures close to 0°C and low light intensities (Mann, 1972b). The growth pattern also differs; the holes punched in the laminae of Phyllogigas elongated, as in L. digitata (Drew, pers. comm.) whereas in L. longicruris (Mann, 1973) and L. saccharina (Parke, 1948) they remained circular and moved distally along the lamina "the fronds resembling moving belts of tissue". (Mann, 1973). Other species of perennial, sub-littoral seaweeds have been shown to grow throughout the winter:

Desmarestia aculeata	Chapman (1971)
Cystoseira granulosa	Chapman (unpubl.) quoted Mann (1973)
Hikikia fusiforme	Suto (1951)
L. hyperborea	Mann (1973), Luning (1969a)
L. digitata	Mann (1973)

The lamina growth rates, smaller than those quoted for other Laminarians emphasised that the growing season for Phyllogigas even in a good year is only 6 months compared with a much longer period for the other species.

It has long been assumed that the principal site of growth in laminae of Laminaria is the transition zone (intercalary meristem) and the tissue nearest to it (Kain, 1976b). Using the technique of punched holes (Parke, 1948) showed this to hold true in L. saccharina as did Sundene (1964) and Cosson (1967) working with L. digitata. Sundene measured the increase in length of the lowermost 100mm of the lamina and showed that the growth pattern of the two Norwegian populations, a northern and a southern, was different. In southern Norway growth was most rapid from February to April and slowest in late summer when the temperature was highest.

When the temperature decreased in early autumn new growth started again, becoming more rapid in late autumn and winter according to the fall in temperature.

In northern Norway growth was most rapid from March to May after which it decreased rapidly although it was considerable when the sea temperatures stayed low.

The growth rate decreased at distances greater than 50mm from the base of the lamina, as seen in Phyllogigas, the growth period being in the same season (Southern Hemisphere). Cosson had similar results with a maximum in May between 40 and 60mm from the transition zone while growth in other months was within 40mm of the zone. Steinbiss & Schmitz (1974) assumed the first 100mm of a 250mm new lamina of L. hyperborea was the growth zone. Similar results have been recorded for other species. Hayashida (1966) found that the fastest growth of the young lamina of Eisenia bicyclis was within 5mm of the transition zone and Norton & Burrows (1969a or b) showed that in Saccorhiza polyschides 76% of the linear growth occurred within the proximal 25mm of the lamina. In Phyllogigas the zone of maximum elongation occurred between 40 and 70mm from the base of the lamina. Fallis (1916) observed that the greatest growth, in width as well as length usually occurred within 30 to 100mm of the base of the lamina depending on the age of the lamina and its morphology, in several species of Laminaria.

Generally speaking the growth curves presented in Chapter 5 show the typical sygmoid type of curve perhaps most clearly seen in plant 1. The three phases of growth are clearly represented:

1. A 'lag' phase in spring with a fairly slow rate of lamina elongation; September to November.

2. A 'log' phase of rapid elongation during the short summer; November to March.

3. A 'slow' phase from March to the onset of winter when there is no growth at all.

These findings agree with other growth studies, e.g. Jupp (1972) working on L. hyperborea. Parke (1948) only recognised two phases, a fast and a slow, in L. saccharina. Norton & Burrows (1969a) observed the fastest rates of growth in juvenile sporophytes of Saccorhiza polyschides, decreasing as the plants became larger, until eventually it stopped altogether.

The variation in rate of elongation that occurred among the plants studied appears to be correlated to some extent with habitat. Age differences in this case can probably be discarded for two reasons:

1. The width of the fronds were all of the same order (81, 56, 52, 84, 54, 40, 60mm) measured near the frond base.

2. The frequency of the summer storms would ensure that few plants present at this site were over three years old. These storms, together with the presence of sea-ice would also severely limit the seasonal development of sporelings, thus ensuring distinct age classes, rather than year round colonisation. Age classes were however almost impossible to estimate for reasons already described.

The results obtained for width measurements contrast with the work of Parke (1948) working with L. saccharina, where a maximum increase in width was observed in the early part of the growing season. The cessation of growth during the winter months in Phyllogigas prevents a constriction in width as seen in L. saccharina and instead a regular tapering towards the distal end of the frond is produced. (Abrasion of the frond tip appears to have little

effect on growth, and no regeneration was ever observed).

Parke (1948) showed that the rate of frond growth increased with shelter, in marked contrast to the plants monitored at the shallow site in this work. However qualitative observations at the deep site where wave action, storm surge etc., were less showed the fronds to be larger. Also, presumably older, due to the less violent environment, which factor cannot be overlooked, though how great a part age plays in such a situation cannot be determined. There is some evidence in the literature to suggest that lamina morphology is largely controlled by wave action. Svendsen & Kain (1971) have proposed the new form L. hyperborea f. cucullata to describe the phenotype of L. hyperborea found in very sheltered regions in Norway (see also Kain (1971b). These growth forms have tortuous stipes tapering to a large, thin, brittle lamina and are restricted to habitats with little water movement. That turbulence and wave action could influence lamina morphology in Laminariales has been shown conclusively in L. digitata by Sundene (1962, 1964) and in Saccorhiza polyschides by Norton (1969). John (1968) found in transplant experiments with L. hyperborea that wave action could affect morphology and Larkum (1972) has produced convincing evidence from studying sheltered and exposed regions that the lamina morphology changes with depth seen in L. hyperborea are brought about in response to changes in turbulence and wave action rather than light.

Thus the influence of the habitat on the rate of frond elongation is considerable, but to isolate with any degree of certainty the influence of individual factors into which the habitat may be analysed quantitatively is difficult. Two factors do however appear to have some influence.

1. Daylength. There is a very close agreement with the start of growth in 1974 and a daylength of greater than 12 hours. September 20th

saw an equal division of 12 hours light and dark. September 23rd, when the new haptera were first observed had a daylength of 12-2 hours.

2. Presence of sea ice. In 1973 the sea ice was present throughout October and November and into December, by which time the phytoplankton bloom had started (12.12.73) Plant 5 did not show any signs of growth until the beginning of December (in that season), and then at a rate of half that in 1974.

It would appear from this that daylength acts as a 'trigger' provided there are no other constraints acting, such as sea ice.

G. A Comparison of the Productivity and Biomass of Phyllogigas with other species

The data presented in Table 6.1 indicate the productive capacity of Phyllogigas grandifolius and are low in comparison with data for various aquatic, marine and terrestrial communities given by Penfound (1956), Ryther (1959), Newbould (1963), Westlake (1963) and Odum (1973). Gray et al. (1959) estimated the productivity of a Typha reed swamp at 16.8 metric tons dry matter $hectare^{-1}$ $year^{-1}$ and Penfound (1959) quotes a growing season productivity for Typha latifolia of 4.5 $gC.\ m^{-2}.d^{-1}$. Such emergent vegetation is considered to have a relatively high productivity (Newbould, 1963) and the data for Phyllogigas is only one order of magnitude below this. Its net annual productivity at the shallow site was found to be 3.4 metric $tons.hectare^{-1}.year^{-1}$. This is assuming a value of 1 for LAI. The maximum LAI, observed at the deep site where the productivity was not very much less was 4.5. This gives a figure of 15.3 metric $tons.hectare^{-1}.year^{-1}$.

The growing season mean productivity was 2.4 $gC.m^{-2}.d^{-1}$ at the shallow site.

Westlake (1963) gives numerous examples of productivity values for marine macrophytes and suggested the net annual organic productivity of sub-

littoral brown algae ranges from 10 to 31 metric tons. hectare^{-1}.year^{-1}. For L. hyperborea Jupp (1972) records 16.5 metric tons. hectare^{-1}.year^{-1} and Westlake (1963) from data of MacFarlane (1952) quotes an average value of 18 metric tons. hectare^{-1}.year^{-1} for L. longicruris. John (1971) has estimated the net annual production of L. ochroleuca and Saccorhiza polyschides in Spanish populations as 6 to 17 and 5 to 39 metric tons. hectare^{-1}.year^{-1} respectively. The maximum observed annual productivity of Phyllogigas agrees quite well with these figures.

The value of the growing season mean productivity of 2.4 gC.m^{-2}.d^{-1} compares favourably with data in Westlake's review, e.g. L. longicruris with 3.9 gC.m^{-2}.d^{-1} and Pinus sylvestris with 2.0 gC.m^{-2}.d^{-1}. Jupp (1972) quotes the range 1.3 to 2.6 gC.m^{-2}.d^{-1} for L. hyperborea. The value for Phyllogigas is very close to the range of highly productive ecosystems with 2.5 to 10 gC.m^{-2}.d^{-1}, including coral reefs, evergreen forests and areas of intensive agriculture (Odum, 1973).

It would appear that Phyllogigas is a moderately productive alga, given the optimal conditions, for example, of the deeper site. The figure of 15.3 metric tons. hectare^{-1}.year^{-1} for this site compares favourably with the value of 16.5 metric tons. hectare^{-1}.year^{-1} recorded by Jupp (1972) for L. hyperborea though at a shallower depth and in warmer waters. Obviously the effects of ice-scour will limit the productivity of Phyllogigas in shallow waters (see Map of algal distribution, Chapter 2). The sub-littoral environment may appear at first glance to be unfavourable to plant life because of the rapid attenuation of light with depth, but it is probably that conditions are generally less changeable than in the littoral zone where the overriding importance of tidal rhythms imposes a daily flux in temperature, desiccation, etc. (Lewis, 1964). Ryther (1959) has indicated that the high production of benthic marine algae is probably due to the almost maximal

absorption of light in dense seaweed beds and an almost continuous replenishment of nutrients by currents and tides. Chromatic adaptation is undoubtedly one major factor in the successful growth of macrophytic sublittoral algae such as P. grandifolius. The absorption maximum of fucoxanthin at 520mm (Tanada, 1951) is ideally suited for absorption in the waters of Borge Bay, where, like the coastal waters around Northern Europe, the maximum transmission of light is from 500mm to 550mm (Coastal type 4 Jerlov 1951), according to Drew, (pers. comm.). That fucoxanthin can transfer energy to chlorophyll has been demonstrated by several workers including Haxo & Blinks (1950) and Tanada (1951). Blackman and Black (1959) came to the conclusion that, provided nutrients and water are non-limiting the rate of growth of any community with a high Leaf Area Index (LAI) is dependant on incoming radiation. Jupp (1972) observed that the high LAI (3.4 to 7.3 m^2 lamina. m^{-2} sea bed) for L. hyperborea indicated that almost total absorption of incoming radiation occurred in situ. Irradiance measurements under the canopy showed that 93% of the ambient light above the canopy was cut off. Neushul (1957) found that one lamina thickness of Macrocystis absorbed about 33% of incident green light and McFarland & Prescott (1959) recorded zero percentage transmission of white light at one metre depth below a thick Macrocystis canopy. As nutrients in the Antarctic ocean are normally not limiting (Deacon, 1933) the growth of Phyllogigas with its high LAI (4.5 m^2 lamina. m^{-2} sea bed) would appear to conform to Blackman & Black's conclusion (above) as does L. hyperborea. (Jupp, 1972).

The biomass of Phyllogigas recorded at the deep site (10.2m) gave a value of 0.8 kg fresh weight. m^{-2} and an LAI of 4.5. Jupp (1972) reports biomasses of 36.7 kg. fresh weight. m^{-2} sea bed at 3.1m for L. hyperborea and 11.3 kg fresh weight. m^{-2} at 9.1m; LAI values were respectively 7.3 and 3.4. The giant kelp Macrocystis develops very large biomasses off the coast of California and in the Indian Ocean. Biomasses of up to 22 $kg.m^{-2}$ (fresh weight) have been reported off California (Mann, 1973) and 95 to 606 kg. m^{-2} with an average of 140 kg. m^{-2} in the Indian Ocean (North, 1971). The net annual productivity in California was 400 to 820 $gC.m^{-2}$ (Clendenning, 1971).

Intertidal seaweeds such as Fucus and Ascophyllum may occasionally have rates of production comparable with those of kelps. In Nova Scotia the fresh weight may be as high as 32 $kg.m^{-2}$ (MacFarlane, 1952) with an estimated productivity of 640 to 680 $gC.m^{-2}.yr^{-1}$ (Teal, 1962). It has been shown that Fucus and Ascophyllum can double their weight in 5 to 10 days and a natural population was able to fix more than 10 $gC.m^{-2}.d^{-1}$ (Kanwisher, 1966).

No definite conclusions about the effect of depth on the biomass of Phyllogigas can be made, due to the sparse distribution of the plants (see Map, Chapter 2). In L. hyperborea, Kain (1971b) has shown that the density decreases with increasing depth, as has been observed in this study, but the maximum size of the plants becomes smaller. Luning (1970) also reports a decrease in size with depth, though the depths range was much smaller, 2-6m. In Phyllogigas, the deeper plants were seen to be much more massive than those in shallower water. In some areas, for instance the Isle of Man, the lower limit of the plants is determined by grazing pressure acting on the establishment of the species rather than its later growth rate (Kain, 1963). Here, the deepest plants are relatively large and there is very little difference in growth rates over the depth range. Unfortunately, no data is

available at present on the growth rates of deeper specimens of Phyllogigas or on the effects of grazing. Large numbers of sea-urchins have been seen in deeper areas where Phyllogigas was present but nothing is known of their feeding habits. Kain (1971b) also reports deep populations in south-west Norway of L. hyperborea consisting of small slow-growing plants. Conway (1967) comments on the variation in size of L. hyperborea from various depths on Carsaig Island, Argyll. Massive development was observed from 5 to 10m, which had been noted previously by Kitching (1941) and dying out at about 16m, a figure which agrees with Forster's (1955) observations near Dartmouth, Devon. The variation in size from plants of 3-4m found at depths of 5-6m and the undersized, deformed specimens recovered from 15-17m is emphasised. No such deformity was seen in Phyllogigas. John (1969) found that the individual performance of L. ochroleuca remained constant at all depths and the low production at depth is explained in terms of a reduction in the density of individuals rather than individual performance. Kain (1971a) correlates this reduction in density at depth with reduced light at the time of establishment.

The biomass data presented in Table 6.1 show that the overall productivity of the area studied is low compared with other sites. MacFarlane (1952) compared her data with the average Scottish values of 5 to 8kg. fresh weight (Walker, 1954) and attributed the higher productivities in Nova Scotia to the greater tidal exchange in those waters. However, the data of Jupp (1972) is in closer agreement. Luning (1969b) found standing crops of 11.1kg. fresh weight m^{-2} at 2.0m and only 0.1kg. fresh weight.m^{-2} at 5.5m for a L. hyperborea forest in Helgoland.

The figure of 4.5 for LAI of Phyllogigas is in close agreement with the literature. Sesták et al. (1971) quote optimal LAI values of 3 to 6 for

most arable crops and 6 to 11 for grass and fodder crops. Luning (1969b) quotes values of 4.1 and 1.6 at 3.3m in a L. hyperborea forest in Helgoland.

The increase in plant longevity in more northern latitudes has been indicated by Kain (1967) as the main reason for the larger plants found in these latitudes; the same reason may be applicable to the large plants found in high southern latitudes also.

The structure of the L. hyperborea forest indicates that shading effects and factors affecting the mortality of older plants are found (Kain, 1963; Jupp, 1972). Phyllogigas was often seen to exhibit self-shading and with laminae lying coiled up on the substratum, (see Frontispiece).

No correlation can be made between chlorophyll content and depth of Phyllogigas. Drew (1977) found the chlorophyll content of young laminae to be 27.8 ug $Chl.cm^{-2}$ and 32.0 ug $Chl.cm^{-2}$ in old fronds which agrees closely with his (unpublished) data for L. hyperborea of 21.7 and 30.8 ug $Chl.cm^{-2}$.

The value obtained for SLA varied between 0.06 and 0.088 $cm^2.mg^{-1}$ giving values of 2.1 and 2.4 ug $Chl.mg^{-1}$ for the young and old fronds respectively of Phyllogigas, assuming an average SLA of 0.075 $cm^2.mg^{-1}$.

H. Respiration

Much of the work on respiration in the Phaeophyceae has centres on algae of the intertidal rather than the sub-littoral zone. For example, the respiration:temperature (RT) curve of several intertidal algae was shown by Newell & Pye (1968) to be modifiable so that the shallow part of the curve is appropriate to the ambient temperature. This 'adaptability' enables the effects of temperature flux to be minimised. Phyllogigas only suffers a small range of water temperatures annually, resulting in a low respiration rate throughout the year (Fig. 2.1). The winter respiration of Laminaria has been shown to be about half that of the summer by Kanwisher (1966) who also found some evidence for acclimatisation in several intertidal species. Similar observations were recorded by Tikhovskaya (1940) who found low spring (March and April) respiratory rates in L. saccharina coincided with lowest temperatures. Thus, at low temperatures the assimilation:respiration quotient is higher. (Round, 1973). This is in accordance with the Harder-Kniep Theory (Gessner, 1955) first proposed by Kniep (1914) and confirmed by Ehrke (1931) which states that holding the respiratory rate down in the spring produces a high photo-synthesis:respiration ratio accounting for the high growth rates observed. This is particularly true of brown algae in polar waters.

Variation in respiration rates was observed along the length of the lamina of Phyllogigas, with the maximum rate occurring in the lower region about 10cm above the lamina base. The rate then decreased distally. No actively respiring frond apex was observed (of course the apex is the meristem in Fucus) as all the fronds studied had damaged apices due either to ice scour, wave action or abrasion against rocks. Instances where browsing by invertebrates was observed were extremely rare (in single figures). The same can be said for epiphytes; in the vast majority of specimens, Phyllogigas was epiphyte-free, so

frond damage in the areas studied would appear to be caused solely by physical factors.

Phyllogigas does exhibit a high spring growth rate; this is shown by the ^{14}C experiments and confirmed by the in situ growth measurements. However with a low ambient water temperature all year the range of respiration observations was only 3.5 $ugC.cm^{-2}.h^{-1}$. (The upper limit is perhaps erroneously high, as can be seen from Fig. 4.3. Spring 1974 shows levels lower than mid-winter 1974 and as low as winter observations in 1973). Jupp (1972) recorded a range of 12.0 $ugC.cm^{-2}.h^{-1}$ for L. hyperborea. Despite the erratic nature of respiration measured at the shallow site (Fig. 4.3) it does not vary significantly over the year as can be seen from the similarity between the gross and net (gross photosynthesis-respiration) photosynthesis curves.

The observed respiration rate in Phyllogigas is similar to the winter rates of algae in more temperate waters, e.g. around the coasts of Britain (Newell & Pye, 1968; Kain et al. 1976). Montfort, Ried & Ried (1955, 1957) have shown that the thermal tolerance of a variety of algae is apparently determined by genetic factors, being unaffected by exposure to zero temperature ($-1^{\circ}C$ to $+1^{\circ}C$) for 4 to 7 months.

Drew (1977) has demonstrated the effect of increased water temperature on the respiration and photosynethic rates of Phyllogigas and several other Antarctic species of algae. Respiration rates showed a rapid rise in all the species considered up to the maximum temperature used, $30^{\circ}C$. The optimum temperature for photosynthesis was found to lie between 15° and $20^{\circ}C$, after which is decreased. This is in close agreement with other data by Drew (unpublished, quoted in Kain et al. 1976) for L. hyperborea. Drew points out that although his data suggest a theoretically possible northward extension

(into warmer waters) of Phyllogigas and the other algae, the long-term effects of increased temperature might be detrimental. With this in mind, further studies using Phyllogigas were carried out. As an endemic species it was chosen as probably being the most vulnerable to temperature changes. Exposure times were increased from the one hour used above to 6 hours and the maximum temperature 26°C. The results showed the inactivation temperature for photosynthesis to be very clearly delimited; 6 hours at 15°C was tolerated seemingly with no deleterious effects but 6 hours at 18°C totally inactivated photosynthesis. The respiration rate was unaffected after 6 hours at 26°C though disturbance of the respiratory metabolism was detected, first occurring at 18°C. Evidence of this disturbance was shown by the failure of the respiratory rate to drop back to its normal level when the tissue was returned to water of 1°C and by changes in the tissue colour and texture. Jupp (1972) found the respiratory optimum of L. hyperborea to be 9.5°C, lower than Phyllogigas and any further increase in temperature caused inhibition of respiration. Sundene (1964) reports on the effect of temperature on Norwegian populations of L. digitata. In Drøbak Sound (about lat. 60°N) the luxuriant population on a submarine ridge in 1m water was completely destroyed in summer 1959 when sea temperatures of 22° to 23°C were recorded. The next two summers the mean monthly water temperatures were 18°C or below and L. digitata was reported to be growing well. Kain (1967) concluded that the local conditions play as important a part in the establishment of plants as does latitude.

In this study observations at the shallow site showed no differences between seasonal respiration rates. However, at the deeper site, significance tests showed that the seasonal rates were different.

The most obvious reason may be that of situation. The shallow s. in the cove at first glance appears sheltered from the worst of the elements,

the cove being open only to the north. However being on the coast in shallow water the plants there do suffer the effects of wave action, storm surge and surf to a greater extent than at the deeper site located on an offshore rocky outcrop. This factor may contribute to the greater density of plants at the deeper site, which were more massive and suffered less damage from wave action and ice scour than those in the cove. This introduces another factor, that of age.

Phyllogigas proved very difficult to age, and no reliable data was obtained. No growth rings were visible in the stipe as Kain (1963, 1971b) has indicated for Laminaria hyperborea nor was there any regularity in the pattern of growth of the holdfast. Attempts to separate the plants into age classes by lamina thickness proved inconclusive even allowing for loss of the distal and hence older, parts of the frond. The lack of increase on size of the stipes in the plants monitored in the growth experiment and the relatively tiny stipes observed in deeper, massive specimens of Phyllogigas is taken as evidence of not such an active subsurface meristem in the stipe, unlike that reported by Kain (1967, 1971c) for Laminaria hyperborea. Thus no allowance could be made for the effects of age on the rates of respiration and photosynthesis other than qualitative expressions of "older" or "younger" plants based on subjective estimations of overall size.

The direct effect of sea-ice on respiration is negligible, see Figs. 3.4 and 3.5. Its main effect is one of indirect action, for by lowering the water temperature the respiration rate is decreased. The experiments carried out on lamina sampled under open water during the winter (Chapter 4, part II) showed that the presence or absence of sea-ice by itself was not enough to affect respiration, tissue composition and hence productivity.

The comparison of respiration rates at three depths down to 32.3m shows the variations that can occur and hence how depth can influence productivity. The abundance of Phyllogigas at depth bears out the fact that standing crop in terms of fresh weight per unit area decreases with depth; e.g. Walker (1950), for Scottish populations of sub-littoral algae and Grenager (1953) for Norwegian populations. The greatest respiration rate observed in this study and hence the greatest loss of carbon was from 32.3m: 13.25 $ugC.cm^{-2}.h^{-1}$, with the other two samples from 10.8m and 4.6m. having lower, more similar rates, 8.42 and 10.01 $ugC.cm^{-2}.h^{-1}$ respectively. Luning (1971) has shown high respiration rates in L. hyperborea to be associated with fast growth, and not with temperature suggesting adaptation to ambient sea temperature. Without attaching too much significance to one series of results taken in isolation the figures may be explained as follows:

Because of their greater size, especially their greater thickness there will be a greater "respiratory load" on the photosynthesising cells. Jupp (1972) has shown that deep-growing plants have reduced respiration rates and this is seen in comparing the results obtained in Fig. 3.4, respiration analysis for 1974 at Cam Rock. The figures for 10.8m indicate a lower respiration rate than at 4.6m. From Table 3.9 it can be seen that the respiration rate per gram dry weight ($R.R.g.^{-1}$. D.Wt.) is lower at 10.8m than 6.2m by 16% so these latter results at least are in accordance with contemporary opinion. Gail (1972) however working with sub-littoral algae found the respiration rate did not change with depth. The greater loss of carbon by the plants at depth will mean that less is being assimilated and hence the productivity and growth rates will be lower than the other plants as would be expected.

Mannitol as a major metabolite

The nature of the respiratory substrate and the presence of carbohydrates in the Phaeophyceae has been investigated by several workers Black (1950a&b); Haug & Jensen (1954), Jensen (1956), Larsen & Haug (1958), Touster & Shaw (1962), Lewis & Smith (1967), Jackson (1971). The possibility of commercial use of the carbohydrates in brown algae, particularly the Laminariales led to a great deal of quantitative work being carried out on the seasonal variations of the major carbohydrates in such species as L. hyperborea, L. saccharina and Alaria esculenta. Black (1950a) has summarised the findings from 1946-1948. These were that a polyhydroxy alcohol, mannitol, a -1:3 linked glucose polymer, laminarin, and the dry weight followed a similar seasonal pattern showing minima in the spring and maxima in the autumn.

Of the various low molecular weight carbohydrates found in the Phaeophyceae, mannitol occurs most often 27 genera are listed by Lewis & Smith (1967) that contain mannitol and the literature contains only one reference to the absence of this polyol in a member of the Phaeophyceae, (Kylin, 1944). The metabolic aspects of polyols are considered by Touster & Shaw (1962).

Black (1950b) found that mannitol content increased with depth of immersion reaching a maximum at 6-10m and decreasing below that. He suggests day length controls mannitol levels in L. hyperborea, reporting an annual minimum of 8% dry weight for March in the Orkneys and a summer maximum of 35%. Further south in Cullipod the same species had a summer maximum of only 26%. Jupp (1972) found higher concentrations of mannitol at 3.1m in January in L. hyperborea than in plants at 10.7m. This situation was reversed in July, with plants at 18.3m having the maximum level of mannitol.

It is possible that in shallow water, the greater lamina biomass may deplete reserves of mannitol in summer. Luning (1970) showed that the

lamina at depth continues growing after those nearer the surface have slowed down. He suggests that the continued improvement of light conditions at depth in summer allows a greater build up of mannitol compared with plants in shallower water. This will obviously be dependant upon the clarity of the water which has been determined by Drew (1977) to be Coastal Type 4 according to Jerlov's classification quoted in Kinne (1970).

Phyllogigas, monitored at the shallow site showed summer maxima in 1973 and 1974 of 14% and 18% dry weight respectively, falling to very low levels during the winter of around 2%. More work is needed on the winter metabolism of this species.

Kylin (1915) first suggested laminarin as a reserve carbohydrate and Nisizawa (1940) suggested that both mannitol and laminarin are storage substances, this being corroborated by Black (1950b). It has been suggested that mannitol is formed as a secondary product of photosynthesis (Black, 1948) in an analogous way to the formation of starch from glucose in higher plants. It has been proposed that the mannitol is brown algae is synthesised by photosynthesis via three carbon compounds. Yamaguchi, Ikawa and Nisizawa (1969) assumed the formation to be via its phosphate produced by reduction, possibly being catalyzed by a mannitol-phosphate dehydrogenase, of fructose-6-phosphate formed by the condensation of triose phosphate. However the occurrence of the dehydrogenase has not yet been demonstrated in the brown algae (Ikawa, Watanabe & Nisizawa, 1972) but it is still assumed that mannitol in brown algae is derived from this sugar diphosphate and that the immediate precursor is mannitol-1-phosphate.

Bidwell (1958a) working on L. agardhii showed that of the photosynthetically fixed ^{14}C accumulated in the ethanol soluble fraction, 85% was in mannitol. Rapid incorporation of radioactivity into mannitol during

photosynthesis in Eisenia bicyclis was shown by Yamaguchi et al (1966) and Bidwell (1967) confirmed that mannitol was in fact the primary product of photosynthesis in brown algae, in at least seven genera (Bidwell, 1958) and contemporary opinion is that it is the primary respiratory substrate. Vaughan, quoted in Parker (1966) found that mannitol was more rapidly consumed during dark periods than other carbohydrates in Macrocystis.

Often large concentrations of mannitol are found in the Phaeophyceae and it has been suggested that much of the mannitol synthesised in photosynthesis is stored or redistributed to build up insoluble compounds. (Jupp, 1972) Quillet (1957) has suggested the steps from mannitol to laminarin via a preliminary oxidation to fructose and then an isomerisation to glucose which is then polymerised to laminarin. Yamaguchi et al (1966) suggest an interconversion occurs between mannitol and laminarin.

In this work laminarin was not monitored, though in many of the above studies, e.g. Haug & Jensen (1954) it was seen to exhibit parallel variation with mannitol. In South Africa, with less marked seasonal variations a winter mannitol maximum and an insignificant laminarin change has been demonstrated by Holdt et al (1955).

The reproductive status of the plant has also been shown to affect mannitol levels. The drop in level observed in Phyllogigas during August and September 1974 may be due to the development of reproductive structures as there is no lamina growth at this time. (See discussion of in situ growth experiment). Moss (1948, 1950) showed the vegetative thalli of Fucus lost their negative concentration gradient of mannitol, from apex to base, at the start of reproductive growth. The mannitol content of the receptacles diminishes with maturity and it has been suggested (Moss, 1950) that the mature gametes do not store this polyol.

The role of laminarin and the relationship between it and mannitol is still not clear. Bidwell (1967) has refuted the idea of interconvertibility and found no increase in the specific activity of complex compounds in sufficient quantities in dark periods for them to be considered analogous to starch in higher plants.

Two other polyols are known in the Phaeophyceae.

1. Volemitol, found in Pelvetia canaliculata (Lindberg & Paju, 1954), the only example of a hepatitol known in the group.

2. Laminitol, a cyclitol found in L. hyperborea (Lindberg & McPherson, 1954), Fucus spiralis and Desmarestia aculeata (Bouveng & Lindberg, 1954). It is present only in trace amounts and like volemitol, has no known metabolic role. (Jackson, 1971).

A COMPARISON OF THE ASH AND MANNITOL CONTENT OF THE LAMINAE WITH PHOTOSYNTHESIS

In general, the ash and mannitol graphs are the inverse of each other in Phyllogigas, when the ash is expressed on a fresh weight basis. The ash content of the fronds shows very little variation when expressed as % dry weight. This agrees with the calorific content expressed in terms of dry weight. Black (1950a or b); Black & Dewar (1949) observed the inverse relationship under the opposite conditions, with the ash expressed on a dry weight basis and Jensen & Haug (1956) showed that this correlation disappeared when fresh weight was used. Why Phyllogigas should be different is not known. The two maxima on the graph for ash weight expressed as % fresh weight may be explained as a result of the frond taking up water at the start of the growing season, even though the sea ice was present in both cases. Certainly in 1974 growth had been observed in September, the time of the maximum. The uptake of water would lead to expansion, producing an increase in surface area. This would lead to increased photosynthesis by reducing the respiratory load. The ash content then decreases for the rest of the growing season, while the mannitol increases, as would be expected, showing a close correlation with photosynthesis. Baardseth & Haug (1953) demonstrated considerable variation of these factors within samples of several species of seaweed.

APPENDIX 1

DIVING PROCEDURES

I INTRODUCTION

Diving at Signy Island was conducted according to the principles laid down in the Underwater Association Code of Practice for Scientific Divers, (ed. Flemming, 1972). With sea temperatures at or below 0°C for much of the year, cold became a serious limiting factor on any dive. 6.5mm. wet suits were worn (long-johns, jacket with attached hood, mitts, etc. and often a 2mm. vest), also Admiralty pattern dry suits and Poseidon 'Unisuits' were used successfully. Care was always taken to prevent excessive cooling of divers after a dive, which might lead to exposure. Fast transport back to base was essential, and in the case of dives further away from base, plenty of warm protective clothing.

II DIVING DURING SUMMER

Open water around Signy Island can usually be expected between November and April, though large variations on these times are possible. Diving in Borge Bay (in sight of base) was carried out from a Zodiac inflatable with an 18hp. 'Evinrude' outboard motor. Further away from base one of the heavier wooden dinghies was used (always carrying a spare motor). The restriction on the Zodiac was due to its extreme lightness and its ability to drift rapidly before the wind. As there was little room for a spare motor aboard, rowing could not prevent drifting in the event of engine failure.

Semi-permanent moorings were usually laid at regular diving sites, such as the shallow site in Factory Cove in this work. These moorings usually consisted of a length of polypropylene rope attached to a rock or heavy weight, and trailing on the surface. No float was used as they were liable to be carried away by pack-ice. If a float was necessary, for instance for suspending equipment from the surface, then a weak link was always fitted between it and the main rope. All moorings were raised before the sea-ice formed. Another advantage of moorings was that divers were not tired out by swimming on the surface at the beginning and end of a dive.

At other sites, without a mooring, one of the divers towed a small marker float and the boatman, circling the boat at a safe distance could watch this, in case the divers needed to be called up quickly. This could happen for instance on the approach of a Leopard Seal or a sudden deterioration in the weather. The revving of the engine up and down was the signal to surface. Buddy lines were worn in less than 3m. visibility, and dives finished when the first diver was down to 50ats. in his cylinder. This left plenty in reserve in case the boat had trouble picking the divers up.

Searches for lost equipment were obviously easier during winter with the excellent visibility (often in excess of 50m.). In summer, depending on the area to be searched and the tidal stream, one of three methods were used:

1. A circular search of a small area, with rope and compass.
2. For a larger area a bottom jackstay, say 100m. long was laid and a team of divers swam up one side and down the other.

3. Towed diver searches using one of the wooden dinghies and in good visibility. Depth was controlled by the speed of the dinghy; up to 4 knots, and communications by a life-line and an agreed set of signals.

III DIVING DURING WINTER

With the ice thick enough to walk on (5-10cm.) divers could not break through from underneath, even with the aid of a knife. When the ice reached its maximum thickness of a metre during the winter months, the only way out was through the hole cut for entry.

Holes 1m. square were cut in the ice with a chain saw and the blocks pushed under the lip of the hole. This size was found to be ideal for ease of entry and exit and with a prominent marker flag flying, did not constitute a navigation hazard to people and vehicles crossing the ice.

Every diver was on a safety line to the hole and that line was tended by a linesman familiar with under-ice diving. The line was always in the hand during a dive held so that the linesman was in direct contact with the diver, but not taut enough to impede him. This line was the divers primary safety measure; "buddy" breathing under the ice being regarded as impractical. With this in mind, the length of line was limited to 40m. (120ft.) a distance which could be covered by a diver out of air while being pulled in by the linesman.

The number of lines at a hole was limited to two, preventing undue tangles. 'Buddy' lines of 4m. (12ft.) were used extensively, secured at either end by snap-links to divers' harnesses. The least experienced diver was on the 'main' line to the surface. A 'sliding' buddy line was sometimes used, one end being clipped to the 'main' line, allowing a diver to swim up and down at will; useful when collecting samples or taking photographs. No more than two buddy lines were used on any dive.

The signals used were limited to two:

3 pulls	–	I am coming up
more than 3	–	Emergency

A.B.L.J's. were not used under ice, for obvious reasons, except for dives below 20m. and then only with experienced divers.

Transport of divers during winter was by a 12ft. Nansen sledge towed by a Ski-doo (snowmobile). Divers were always fully dressed before leaving base including mitts, as hands cold before a dive would not warm up. In very cold weather, contraction of metal parts could loosen divers' hoses or even the regulator on the pillar valve. These were checked by the linesman on request.

Deep diving (below 30m.) was only undertaken by experienced divers after a number of "work-up" dives either in the sea or in the recompression chamber. The system used was based on that employed by the Royal Navy. A qualified diver acting as Supervisor on the surface worked out decompression times from the deepest water dived in, measured beforehand with a shot-line. On the dive, two divers went down on a line and 'buddy', the linesman giving one pull every minute and the divers replying. If there was no answer the divers were pulled up. At two minutes to decompression time 2 pulls were given and replied to. A 5 minute stop at 10ft. was always carried out as an extra safety measure with a spare set lowered to the divers in case it should be needed.

If the divers stayed into decompression time then the Supervisor worked out the decompression and the divers were raised on the shot-line from the surface, at each stop. The recompression chamber was made ready for immediate use and the Supervisor was in contact with the base by radio. All base personnel including non-divers were instructed in the use of the chamber. See also Fane (1959) and Neushul (1961).

APPENDIX 2

THE CLIMATE OF THE SOUTH ORKNEYS

The surrounding ocean plays a major role in reducing the severity of the climate of Signy Island. As a result relatively high air temperatures with a small seasonal range together with the consequent availability of rain and melt-water have permitted the development of a rich and varied flora. In common with other regions within the maritime Antarctic at least one of the summer months has a mean sea-level air temperature above freezing point, while in winter the mean for the coldest month is seldom below -15°C. Mean monthly meteorological data for a 20-year period for Signy Island and a 46-year period for Laurie Island (the second largest island in the South Orkneys) are summarised in Table 1, with further data given in Table 2.

The prevailing winds on Signy Island are from south-west to north-west while in addition there are frequent warm northerly winds resulting from Föhn effects created by the 1000 to 1,200m. mountain barrier of central Coronation Island. Frequent heavy cloud cover and lack of sunshine are typical features of the climate and give a high frequency of precipitation.

From early December to late March air temperatures frequently rise above 0°C and mean temperatures may be above freezing point for 1-3 months during summer. On calm, sunny days ground temperatures may briefly exceed 30°C as rocks, soil and plant surfaces are warmed by incident radiation. In summer considerable areas of the lowlands become clear of snow and even in winter katabatic winds may cause an increase in temperature of 20°C in a few hours, producing temporary thaws. Most of the ground is covered by

varying depths of snow throughout much of the winter and although the air temperature may fall below $-30^{\circ}C$, the temperature

	Air Temp.(°C)		Wind Speed(M.sec^{-1})		Relative Humidity %		Sunshine(hrs.)		(mm) Precipitn.
	Signy 48–67	Laurie 04–50	Signy 48–65	Laurie 04–50	Signy 48–61	Laurie 04–50	Signy 48–66	Laurie 04–50	Laurie 04–50
J	0.78	0.11	6.0	4.1	85	85	2.3	1.5	35.2
F	0.87	0.23	7.3	4.8	85	86	1.7	1.4	39.1
M	0.29	-0.57	7.7	5.0	87	86	1.2	1.1	47.9
A	-2.27	-3.32	7.9	5.4	86	86	1.0	0.8	41.4
M	-6.22	-7.12	6.7	5.3	85.5	85	0.7	0.55	31.6
J	-7.96	-10.37	6.7	4.8	86	85	0.4	0.3	26.0
J	-10.28	-10.87	6.6	5.1	84	83	0.9	0.6	31.7
A	-9.38	-10.22	7.0	5.3	85	84	1.6	1.4	31.8
S	-5.34	-6.92	8.8	5.5	86	84	1.9	1.2	28.7
O	-2.75	-3.93	9.1	7.7	86	86	2.1	2.2	29.0
N	-1.38	-2.30	7.8	4.8	86	86	2.2	1.8	32.2
D	-0.18	-0.77	6.2	4.0	87	85	2.0	2.0	26.5
Annual Mean	-3.65	-4.67	7.3	5.0	85.5	86	1.55	1.3	33.4

Table A21 Mean monthly climate data for Signy and Laurie Islands, 1948 to 1967 and 1904 to 1950 respectively.

on the moss surface under the snow rarely drops below $-1.5^{\circ}C$ except where the snow protection is lacking.

The extent to which winter snow disappears during summer depends on the length of time temperatures are above freezing and on the amount and frequency of rainfall. For example the most extensive retreat of the snow line on Signy in recent years (possibly excluding 1974–75) was in 1964–65 following mean monthly air temperatures of 0.5°, 2.2°, 2.8° and $1.8^{\circ}C$ (mean $1.8^{\circ}C$) for the months December to March respectively. During the

summer of 1965-66 the mean temperature for the same period was 0.4°C when there was a very gradual and much less extensive disappearance of snow and a number of the freshwater lakes remained frozen throughout the year.

	Signy (14 years)	Laurie (46 years)
No. gales	63	N.D.A.
No. cloudy days 20 octas	258	288
No. clear days 4 octas	7.5	4
No. days with snow	259	262
sleet	57	N.D.A.
rain	76	"
drizzle	100	"
Total equivalent rainfall (mm)	no data available	398

Table A2.2 Mean annual climatic data for Signy and Laurie islands.

APPENDIX 3

SEA-ICE

I FORMATION OF SEA-ICE

The main factor in the freezing of sea-water is a drop in air temperature. The first sign of sea-ice is a scum of fine spicular crystals or plates of ice in suspension giving an oily or opaque appearance to the surface of the water: frazil crystals. This stage, in calm cold weather conditions will be followed by a thickening of the scum to form a soup of crystals: ice slush, which will finally consolidate into a thin elastic sheet of ice normally less than 5cm. thick: ice rind.

All this process has been due to a low air temperature freezing the sea, but now there is a firm layer of young ice which can thicken both by the addition of further ice to the underside or by snow falling on the upper surface. In this manner the ice may become thicker throughout the year although the rate of growth from the underside will decrease as the ice thickens. (For a more detailed description of the formation of sea-ice see the "Antarctic Pilot, 1963, p31).

At any point in this process of thickening the ice may be broken up by the wind which can either disperse the resulting pack-ice completely or merely jostle the floes together, turning up their edges and allowing them to refreeze when the wind has dies down. This is a usual phenomenon in the case of ice rind which has little strength and which when broken up produces pancake ice.

If sea-ice is subjected to lateral pressure the resultant formation

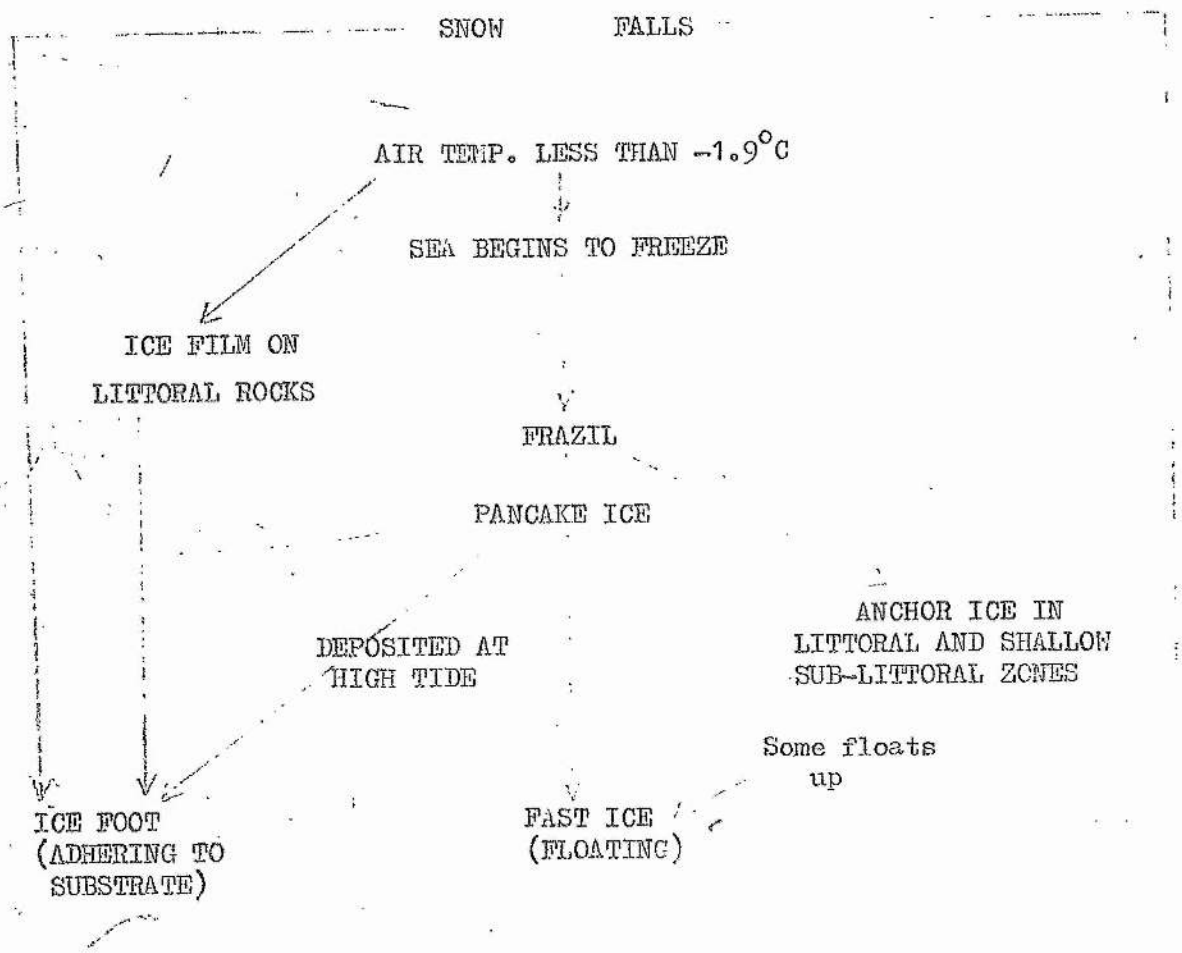

Fig. A3.1 Sea-ice formation in the littoral zone.

depends to some extent upon the thickness of the ice. If the ice is thin, up to about 5cm. then the most normal result of pressure is rafting. This process can be likened to the pushing together of a deck of splayed-out playing cards and can very quickly increase the thickness of the ice. The process of hummocking occurs when the the ice is thicker than new ice. Pressure ridges, usually arranged at right angles to the line of action of the force are formed when the ice thickness is more than 10cm. The ridges are usually lines of weakness despite their very great thickness, often reaching heights of 3m. above the surrounding level which probably represents an extension below the surface of four or five times that above.

II DECAY

In the spring and summer the ice around Grahamland (the Antarctic Peninsula) decays, breaks up and is dispersed. Although there is much information on the decay of ice in Arctic waters, there is very little of a comparable nature for the Antarctic. Essentially the problem is this: while the ice is thickening it will be increasing its resistance to wave action. If no increase in the power of storms is postulated (i.e. no increase in the power of wave action) the fact that the ice does break up in the late spring must indicate that some process has been active which weakens the ice. Basically this weakening may proceed in three ways:

1. Ice may be removed from the underside by the melting action of the sea.
2. Snow, and later, ice may be removed from the upper surface by the evaporation (ablation) induced by the increasing power of the sun. Straightforward thawing, producing water may also take place.

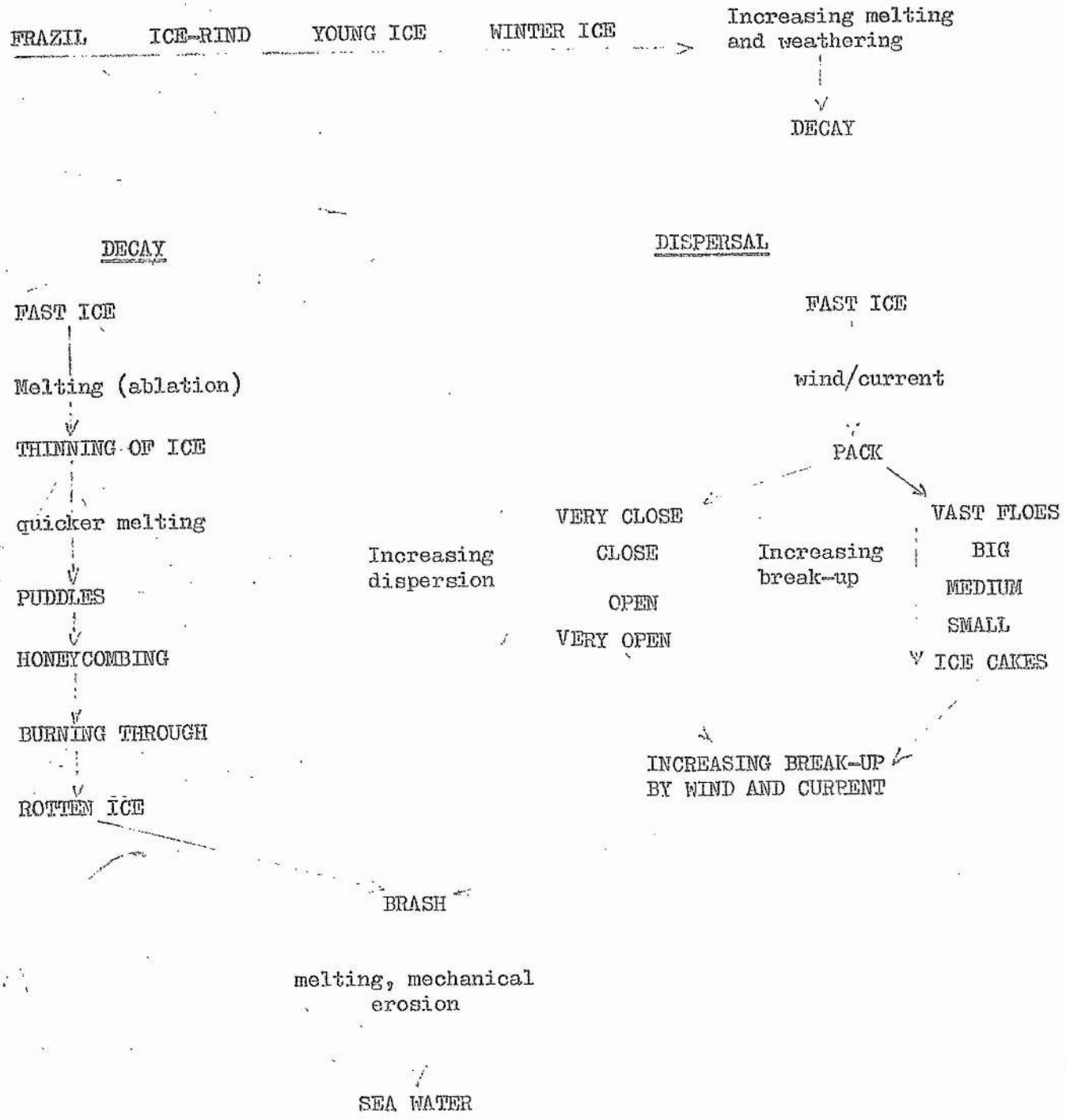

Fig. A3.2 Stages in the decay and dispersal of fast-ice.

3. Although some of the salt in sea water is excluded in the process of freezing some remains included in the sea-ice causing patches of ice that are particularly briny. This ice melts at a lower temperature than brine-free ice; e.g. $-1.5^{\circ}C$ say as opposed to $0^{\circ}C$. Hence when the summer temperatures have slightly warmed the whole ice mass differential melting will take place and patches or layers of water will form in the ice body thus reducing the strength and cohesian of the whole mass. No simple observations can be made to measure the degree of weakening induced by this method. This differential melting causes the honeycombed appearance of rotten ice.

Signs of ablation and thawing may also be seen on the surface of sea-ice. Snow that is melting will turn from a fine powdery or granular nature to a sticky almost slushy consistency and may later melt completely to produce puddles over the surface of the ice. Later when bare ice is exposed, briny ice melts under the sun producing honeycombing. This is less common than in the Arctic.

III DISPERSAL OF SEA-ICE

When the fast ice breaks up the resulting ice floes and pack will be moved by wind and current. Because of the large surface area a floe presents to the wind and because wind speeds are many times the speed of currents, pack is more subject to movement by winds than currents. If the surface of the ice has been roughened by pressure then each ridge or hummock will act as a sail for the wind to catch. In open water differences in wind resistance will result in different speeds of movement before the wind, causing greater dispersal. Pack will thus tend to decrease in concentration the further away it moves from its source as long as it is free to move. It is frequently observed that pack composed of floes of roughly equal size moves about

the open sea as strips lying approximately at right angles to the wind direction.

It is possible that an increase or decrease in the number of 'bergs drifting around the Weddell Sea and the western peninsula area may have a significant connection with 'warm' and 'cold' years experienced in the peninsula. Iceberg numbers may therefore prove to be of climatological importance.

TABLE A3.1 SEA-ICE RECORD FOR FACTORY COVE 1974

(Depths of snow, slush and ice in cm.)

DATE	SNOW	SLUSH	ICE
23. 4.74	0	10	0
3. 5.74	0	4	0
4. 5.74	0	3	0
12. 5.74	0	1	0
13. 5.74	0	0	0
14. 5.74	0	0	0
15. 5.74	0	1	0
16. 5.74	0	3	0
17. 5.74	TR	0	7
18. 5.74	TR	0	8
19. 5.74	TR	0	8
20. 5.74	TR	0	8
21. 5.74	TR	0	9
22. 5.74	TR	0	8
23. 5.74	TR	0	8
24. 5.74	1	TR	13
25. 5.74	1	0	14
26. 5.74	TR	TR	18
27. 5.74	TR	TR	19
28. 5.74	TR	TR	20
29. 5.74	3	1	20
30. 5.74	4	1	22
31. 5.74	2	2	22

NOTE: 'SLUSH' COLUMN INCLUDES FRAZIL AND GREASE ICE DURING INITIAL STAGES OF GROWTH (TR = TRACE)

FACTORY COVE 1974

	JUNE			JULY		
DAY	SNOW	SLUSH	ICE	SNOW	SLUSH	ICE
1	7	3	23	1	0	31.5
2	7	3	23	1	0	31.5
3	7	3	23	1	0	31.5
4	8	2	23	3	0	32.0
5	10	2	23	3	0	32.0
6	9	2	23	3	0	33.0
7	6	1.5	24	3	0	33
8	7	0	23	3	0	33
9	7	0	23	8	0.5	33
10	6	0	23	7	0.5	33
11	6	0	24	7	0.5	33
12	7	0	25	7	1	33
13	7	0	25	8	1	33
14	7	0	25	11	2	33
15	7	0	26	11	4	33
16	7	0	27	12	7	33
17	8	1	28	19	2	33
18	8	1	28	18	1	34
19	8	1	28	17.5	1	34
20	7	1	28	17	1	34
21	7	1	28	8	1	34
22	9	2	28	7	1	34
23	10	2	28	11	1	34
24	9	1	28	10	1	34
25	9	1	28	10	2	34
26	9	1	28.5	14	2	34
27	4	1	29.0			
28	0	0	29.5			
29	0	0	31.0			
30	0	0	31.5			
31						

	AUGUST			SEPTEMBER			OCTOBER		
DAY	SNOW	SLUSH	ICE	SNOW	SLUSH	ICE	SNOW	SLUSH	ICE
1									
2									
3									
4							15	0	70
5									
6	7	11	47						
7									
8									
9									
10							6	0	76
11				19	0	68			
12									
13									
14									80
15	2	7	60						
16									
17									
18									
19				9	0	70			
20	2	0	65						
21									
22									
23	12	0	57				0	0	73
24									
25									
26									
27									
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